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THE ANATOMY OF THE CONIFERALES.

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(*Continued from page 554.*)

RESIN PASSAGES.

Distribution and Taxonomic Value.

PRANTL (44, p. 37) states that resin passages occur in the wood of "most Abietineæ, namely, Pseudotsuga, Picea, Larix, Pinus and *Abies firma*." This statement requires some modification in detail, especially with respect to the last named genus, and in order to make the results of the present studies clear it will be expedient to discuss separately the distribution of the resin cysts and the resin passages.

The first species to which our attention may be directed is *Tsuga mertensiana*. This is the only species of the genus in which definite resin cysts are to be found. Such structures are never numerous, and they take the form of short rows of contiguous cysts in the initial layer of the summer wood of distant growth rings. Longitudinally they have no definite limits, but they appear to be extended for great distances, and probably

through the entire longitudinal growth of the season, at least. There is no obvious alteration either in the position or volume of the resinous contents of the isolated resin cells which lie on the outer face of the summer wood. The constancy with which these structures occur gives to them a definite value for the recognition of the species, and permits us to differentiate it from *T. caroliniana* on the one hand and from the remaining three species on the other.

In the genus Abies only four species out of eleven show resin cysts. These are *A. bracteata*, *A. nobilis*, *A. concolor* and *A. firma*. Referring again to Prantl's observation (44, p. 37), it must be pointed out that his statement with respect to the occurrence of resin passages in *A. firma* requires modification in detail, in so far as these structures are not passages but cysts; while he also appears to have overlooked the occurrence of similar structures in the three other species mentioned. In all of these cases the cysts are contiguous and disposed in tangential rows of considerable length, either in the summer wood (*A. concolor* and *A. nobilis*), in the outer spring wood (*A. firma*), or in both the spring and summer wood (*A. bracteata*). Such variations appear to be of no specific value, conforming as they do to similar variations in the zonate distribution of the resin cells. It is found, however, that in only one case (*A. concolor*) are these cysts associated with isolated resin cells. In the three other cases the resin cells are entirely wanting, a relation which is strongly suggestive of their replacement by the cysts.

Sequoia sempervirens is the only species of that genus which develops resin cysts in the secondary wood, though Jeffrey (24) has shown that such structures are normal to the primary wood zone of *S. gigantea*, and not elsewhere. As already shown, such cysts are much more highly organized than those of either Tsuga or Abies, though they are similarly contiguous and even coalescent, and form extensive tangential rows in the initial layer of the spring wood of distant growth rings. They form a much more prominent feature than in any of the preceding species, because of their generally larger size and the greater extent of the series in which they lie. Unlike Abies, however, there appears to be no diminution either in the number or the extent

of the prominent resin cells which are often intimately associated with the cysts.

The normal course of development for such cysts as thus described is subject to special alteration under conditions which involve an unusual stimulus to growth, and under such circumstances they may become definitely associated with, or may even be regarded as indicative of, pathological conditions. Thus Anderson (1, p. 28–29) has shown that such cysts are definitely developed in association with the formation of Witches' brooms in *Abies firma*. Under such circumstances the cysts become much larger, more distant and more numerous than in normal growth, but they form well defined tangential rows in the earlier spring wood of successive growth rings. In the development of such secondary features the cysts manifestly exhibit a distinct approach to that higher type of structure and distribution which is exhibited in Picea. In the following year Anderson (2, p. 336) further showed that while resin cysts are absent from the normal wood of *A. balsamea* they do arise under the influence of the special stimulus connected with the formation of tumors produced by the action of *Æcidium elatinum*. He furthermore points out that such cysts attain their greatest development and largest number in the region of greatest stimulation, *i. e.*, in the middle of the tumor, decreasing above and below until they eventually become pointed and finally disappear between four tracheids "which, in their meristematic condition, probably function as epithelial cells." It is unfortunate that the histological details of these cysts and their endings are not given, since such facts would serve to throw much light upon the relation of the cysts to similar structures in normal tissues, but there is no reason to suppose that they differ in their essential structure from those which occur in the normal tissues of the same or other species. The tracheids above referred to are undoubtedly parenchyma tracheids, and it is probable that further examination would show that they ultimately replace the resin cells remaining over after the disappearance of the cyst proper.

More recently Jeffrey (24) has contributed an important paper on the anatomy of Sequoia in which he brings out several facts of considerable value. He shows that resin cysts may

arise in the roots of *Abies balsamea* which have been injured, while they may also be produced experimentally by injury, thus confirming the observations of Anderson that they may be traumatic in their origin. The most significant facts, however, relate to the normal occurrence of such cysts in Sequoia. He shows in the first instance that they are absent from the wood of the first year's growth in *Sequoia sempervirens*, while they are present for the same period of growth in *S. gigantea*, though absent from the growth of later years. In both species they arise in the earlier spring wood. Jeffrey concludes that the tangentially disposed resin cysts of *Sequoia sempervirens* represent the result of injury, and he would apply this rule to all similar cases in the various species of Abies and Tsuga.

Some years since, De Bary (9, pp. 490 and 495) formulated the law that "resin canals . . . . occur in the ligneous bundles of the same Abietineæ which possess horizontal canals in the medullary rays." This is a law of very great constancy, and, as recently shown by Penhallow (39), it is applicable without exception to all living species. But as the same author (41, p. 42) has shown more recently, *Sequoia burgessii* from the Eocene of the Northwest Territories offers a remarkable exception to this law, since it shows well defined resin passages in the medullary rays, but without corresponding structures in the vascular bundles.

As presented by existing species, Pseudotsuga, Larix, Picea and Pinus, without exception, show resin passages in both the radial and longitudinal positions. In transverse section they are scattered throughout, sometimes appearing chiefly in the summer wood, sometimes chiefly in the spring wood, or again about equally in the two regions, and they rarely conform to the precise law stated by De Bary (9, p. 495), that "they lie scattering in a ring in the external region of every annular layer." The constancy of their occurrence in the four genera mentioned involves very few features which call for special comment. In Pseudotsuga and Larix the resin passages are scattering. Sometimes they not infrequently unite in pairs so as to form short, tangential series and they thus approach the type of Tsuga or Abies, while yet again they may become definitely iso-

lated and scattering, thereby approaching the distribution of Picea and Pinus. In *Larix occidentalis* the tendency to a primitive form of distribution is expressed in the formation of a tangential zone essentially similar to that of *Tsuga mertensiana*. In both Pseudotsuga and Larix there is an obliteration of resin cells from all parts of the structure except the extreme outer face of the summer wood. In Picea, however, without exception, there is a complete obliteration of all resin cells except such as enter into the structure of the resin passages, and this is directly correlated with a higher type of structure in such passages.

In the genus Pinus, as already shown, the resin passage reaches the highest degree of organization in all respects. It shows little if any tendency to those primitive associations which are expressed in the formation of tangential series, while it has entirely replaced the isolated resin cells which are never to be found in that genus.

If, then, we ask what value such structures have for taxonomic purposes we find them to be of well defined importance. It has already appeared that in Tsuga the occurrence of resin cysts is of well defined value for specific differentiation, and the same rule is also applicable to *Sequoia sempervirens* and to four species of Abies. In the higher Abietineæ, inclusive of Pseudotsuga, Larix, Picea and Pinus, the invariable association of resin passages in the wood and in the medullary rays not only serves to separate these genera from all those in which resin cysts only may occur, but it differentiates them absolutely from all the remaining genera. Such association therefore constitutes a feature of great value. More particularly, the thin-walled epithelium of Pinus at once separates that genus from the other three, which are invariably characterized by thick-walled epithelium. Such generic differentiations are greatly emphasized by the occurrence of thyloses. These are typically developed in Pinus, where they are always thin-walled and almost invariably present. They are therefore of definite value as supplementing other features previously described. In the other genera, however, their presence in either the cyst or the resin passage, where they are generally thick-walled, is of so sporadic a nature as to give them no definite value, and we therefore find that for specific diagnoses such structures may be neglected.

PHYLOGENETIC.

We are now in a position to present an answer to the question, "How are the resin passages related to the phylogeny of the Coniferales?" In order to present an intelligent answer to this question it will be necessary to recall the facts already discussed in connection with the resin cells and bring them into relation with our discussion of the resin passages.

In the genus Sequoia it has been shown that the general course of development of the resin cells is essentially the same as in Cupressus, etc., while it has also been shown that the genus presents in other respects a somewhat remarkable deviation. Of the two existing species, both show the distribution of the resin cells to be of the typically primitive form, *i. e.*, scattering. Nevertheless there are also in *Sequoia sempervirens* definitely organized resin cysts but without exhibiting the transitional form of a zonate disposition. Among fossil representatives Penhallow (41, p. 41) has shown precisely the same feature to be present in *S. langsdorfii*. This is the less remarkable, however, because that species is undoubtedly the ancestral form of, and practically identical with, *S. sempervirens*. The fact made clear by Jeffrey (24, p. 457), that resin cysts occur in the first annual ring of vigorous branches of adult trees, as well as in the roots of *S. gigantea*, also tends to make it apparent that the genus presents a very striking advance upon even the type presented by Juniperus, since the aggregation of resin cells and the formation of cysts from them has arisen abruptly and without the transitional forms presented by Juniperus and Taxodium. While, therefore, Sequoia is obviously related to Thuya and Cupressus on the one hand, it is on the other hand related to such types as Abies. In this sense it may be regarded as the terminal member of a developmental series embracing the Taxodiinæ, Cupressineæ, Taxoideæ as follows:—

1. Taxus and Torreya.
2. Thuyopsis.
3. Cryptomeria.
4. Podocarpus.

5. Cupressus.
6. Thuya.
7. Libocedrus.
8. Taxodium.
9. Juniperus.
10. Sequoia.

In the Abietineæ a new series is presented. This is not in any sense strictly coterminous with the first, but the two appear to make a fault, as it were, whereby there is a lateral displacement, but of such a nature that Sequoia still serves as the connecting link. Within the eleven species of Abies investigated three important phases are presented: (1) Resin cells scattering on the outer face of the summer wood, (2) resin cells grouped and forming cysts, and (3) resin cells entirely wanting. Viewing these phases in the order given, it is to be observed that in those four species which develop cysts only one shows isolated resin cells, and it is probably correct to interpret the variations noted as expressions of developmental phases in such a way that the occurrence of cysts represents the highest position. The genus Tsuga is closely related to Abies in the occurrence of isolated resin cells on the outer face of the summer wood, as also in the formation of resin cysts, but it obviously occupies an inferior position because (1) of the greater abundance of resin in the individual cells, and (2) the occurrence of definite aggregates of resin cells without the formation of cysts. This series is directly extended by those genera in which definite resin passages replace the simple cysts, since the latter are convertible into the former by easy and natural transitions. Both Pseudotsuga and Larix occupy equivalent positions because they not only present resin passages of an equal degree of development, but they show a survival of the isolated resin cells on the outer face of the summer wood. Their affinities are therefore directly with Abies and Tsuga on the lower side, but on the upper side their alliance is with Picea, which presents a very similar though somewhat higher organization of the resin passage and a complete obliteration of the isolated resin cell. Yet again, the structure of the resin passage in Picea at once connects that genus with

Pinus, in which the most complete development is attained, and it therefore terminates the series upwardly.

Having special reference to the particular forms of the secretory reservoirs, and leaving out of account all other considerations than their particular evolution, it is possible to indicate the general sequence of the genera and, to a more limited extent, of their species, as follows: —

1. Tsuga caroliniana.
   " mertensiana.
2. Abies bracteata.
   " firma.
   " nobilis.
   " concolor.
3. Sequoia.
4. Pseudotsuga and Larix.
5. Picea.
6. Pinus.

From this it is manifest that Sequoia is superior to Tsuga and Abies but inferior to Pseudotsuga, Larix, etc. But if we now view the general phylogeny with reference to the entire course of development of the resin cells and the resin passages, the relations just explained must be modified with reference to the particular position of Sequoia, and the sequence would then become: —

1. Thuyopsis and Cryptomeria.
2. Podocarpus.
3. Cupressus.
4. Thuya.
5. Libocedrus.
6. Taxodium.
7. Juniperus.
8. Sequoia.
9. Tsuga.
10. Abies.
11. Pseudotsuga and Larix.
12. Picea.
13. Pinus.

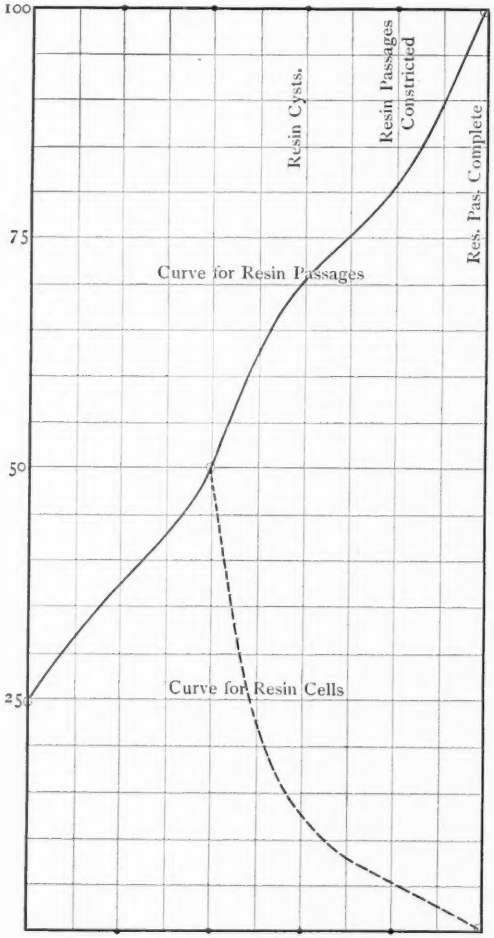
But it may assist in the general argument to view this question from another standpoint. Regarding the resin cells and the secretory reservoirs as falling within a definite series, we may apply to the various forms of distribution and to the various grades of resin reservoirs arbitrary values of such a nature as to represent our conception of their relative positions in the scale of development as expressed by percentages, thus: —

Resin cells scattering	25.0%
" " zonate	37.5 "
* " " grouped	50.0 "
" " on the outer face of the inner wood, Pseudotsuga and Larix . .	12.5 "
" " on the outer face of the summer wood, as in Abies (partial only),	5.0 "
" " wholly wanting	0.0 "
†Resin cysts, as in Tsuga, Abies and Sequoia .	70.0 "
Resin passages with constrictions, as in Pseudotsuga, Larix and Picea	80.0 "
Resin passages without constrictions and of the highest type of organization, as in Pinus .	100.0 "

We obviously have two subordinate series here, which for convenience may be regarded as coterminous, but which as already shown are "faulted" in such a way that the grouped resin cells (*) and the resin cysts (†) jointly represent the point of divergence for two separate courses of development, the latter continuing upward, while the former descends and thereby represents degradation. These features are best exhibited graphically, and the accompanying curves clearly show how, on the one hand, resin cysts and resin passages directly result from special modification of cell aggregates, while on the other hand, from the same starting point, there arises a course of degradation which finally results in the complete obliteration of the resin cell as an independent structure.

The facts thus far set forth have thrown important light upon the general course of development of certain anatomical features, and they also show the general course of development for genera

and species with reference to particular structures. They do not, however, convey any information with respect to the origin



Curve showing the approximate development of resin passages, and the corresponding obliteration of resin cells.

of the phylum as a whole, or the relations of the particular genera and species from the standpoint of collective data, and such a

discussion will be more appropriately reserved for the general summary. There is, however, one feature arising out of recent investigations which calls for consideration at this point, since certain of the conclusions reached are not in harmony with our own, the divergence of opinion indicated being the result of different methods of interpretation.

Jeffrey states (24, pp. 447 and 457) that *all* such resin cysts as occur in *Sequoia sempervirens* and Abies are of a traumatic nature, and therefore pathological. To this category he would also doubtless assign the corresponding structures of Tsuga. This opinion appears to be shared by Anderson (1 and 2), and it is also apparently supported by Pierce (42). Both Jeffrey and Anderson show that the development of such cysts is sometimes definitely associated with the production of tumors through the operation of parasites, and that they may also be induced by wounds experimentally produced. The facts they cite show conclusively that resin cysts may, and often do, arise traumatically, but in such cases they lie outside the usual course of development.

The occurrence of resin passages in the fundamental tissue of the Coniferales is a well known fact, as pointed out by De Bary (9, p. 441) many years since, when he summarized the general facts in the statement that "all investigated species of Coniferæ, with the single exception of Taxus, have resin passages or resin reservoirs which vary in distribution and number according to the species." This statement would include the leaves and bark and sometimes even the pith of species which produce neither isolated resin cells nor resin reservoirs of any kind in the xylem tissue of the stem. It directs attention somewhat forcibly to the fact that while the occurrence of resin reservoirs in the fundamental tissue is a legitimate inheritance of the mucilage canals of the Eusporangiate ferns and the Cycadofilices, as also later of the resin cells of Cordaitales, the xylem structure is the very last to receive the impress of such a course of development; and it is therefore in nowise surprising that the resin passages do not appear there until a very late period of development and that their organization can even then be brought about only through a somewhat prolonged series of changes which are initiated by the occurrence of isolated resin

cells, much as the formation of mucilage canals may be traced back to specialized cells which separately have the same function in the Eusporangiate ferns.

The local occurrence of resin passages in the xylem of the floral axis in no way invalidates the obvious conclusions to be drawn from these statements, since it may be readily accounted for in other ways. In a structure so unresponsive to influences which would induce profound alterations as the xylem, it is to be expected that important structural changes could be effected only after a prolonged interval during which the fixation of any particular character would be preceded by a period of sporadic development within which such character would be liable to recur under special conditions; and as such conditions are obviously of fundamental importance we may inquire somewhat more fully into their nature and results.

The statement of Prantl (44, p. 35) that "those genera which are devoid of resin passages in the wood of young and vigorous growth later produce single parenchyma elements in the wood, which contain resin" requires some modification in view of what Jeffrey has shown in the case of Sequoia and Abies, as well as what has been shown in the course of the present studies, and in its more comprehensive and exact form it should read, "those genera which are usually devoid of resin passages in the wood, but some species of which may nevertheless contain resin cysts in the young and vigorous growth, later produce single parenchyma elements in the wood, which contain resin."

Taken by itself this statement as applied to Sequoia and Abies might be held to indicate that the growth of the first year represents the most stable structural region of the entire stem, in the sense that it embodies characters which are most fully established, and that it will therefore embrace elements which may be eliminated from the older parts, or which may be replaced there by degenerate forms only. From this point of view it would be necessary to regard the complex resin passage as the primitive form of structure from which the cysts, groups of cells and isolated resin cells have been derived by a process of progressive degradation. This view appears to have been

adopted by Jeffrey (24, p. 454), who supports his position by citing the occurrence of resin passages in the vascular structure of the peduncle of certain fossil Cycads, interpreting this to mean that such structures represent a survival of features which have been obliterated from the structure of the stem. Such a view does not seem to be in harmony with the facts which our own studies have brought out, to the effect that resin passages of the type found in the xylem structure are in no sense primitive or vestigial, since they are wholly wanting in the primitive gymnosperms, and their organization does not arise until a very late period in the evolution of the highest forms. If our interpretation of observed facts is correct as applied to the origin of the resin passages, it shows as clearly as one could well expect a progressive development from the isolated resin cell through various phases of aggregation to the highest form of structure as found in Pinus. That there is such a series cannot be doubted and we must interpret it in one of two ways: either as progressive evolution or as progressive degeneration. To us the arguments all seem to be very emphatic with respect to lending support to the former view, most especially as all anatomical data confirm the relative positions of the genera as determined by the development of the resin passage. But assuming for the moment that the latter view is the correct one, let us see where it would lead us. It would first of all necessitate a direct reversal of the structural sequence, and this in turn would impose the necessity of placing the genus Pinus at the bottom of the scale, while those genera like Taxus, Torreya, Agathis, etc., which have no resin cells even, would be at the top. I venture to suggest that such a proposition would meet with instant opposition even from the advocates of the idea that the resin passage has preceded the other forms of resin bearing structures. The whole question appears to turn upon our recognition of what constitutes the most impressionable portions of the stem structure, and therefore the regions within which structural changes are initiated. In this connection the evidence of both palæobotany and recent botany brings out certain facts with great force and throws them into strong relief. They are as follows:

1. The mucilage canals of the Eusporangiate ferns may be regarded as the ancestral forms of the resin passages among the higher plants, but they are obviously the successors of, as they are derived from aggregates of, mucilage sacs as simple, parenchyma cells.

2. Resin passages are wholly unknown in the wood of the stem of ferns, the Cycadofilices, the Cycads, Cordaites or Araucarioxylon.

3. Resin cells are known and are abundant in the pith and bark of Cordaites, but they are absent from its wood.

4. Resin passages are known in the bark and in the pith of the Cycadaceæ, of Agathis, Araucaria and of the Coniferales in general. They also occur in the wood of the peduncles of Sequoia and Cycas, and in the xylem of the first year's growth of vigorous shoots in Sequoia and Abies. They likewise occur in the leaves generally.

5. In *Sequoia burgessii* from the Eocene, resin passages occur in the medullary rays, but they do not traverse the wood longitudinally, though isolated resin cells do occur there.

From this it would seem that the fundamental tissue is the most impressionable with respect to the development of these structures, and that after it we have in the same order the peduncle of the inflorescences and the wood of the young shoots, to which latter category would also belong the development of resin passages in fasciated stems, and such a sequence is precisely what we should expect from our knowledge of the relation which the fundamental tissue bears to other structures. According to this conception the resin passages may appear in any part of the woody structure where growth is sufficiently vigorous, but such appearance would be temporary and indicative only of a future course of development which has not as yet become sufficiently well impressed upon the organism to form a permanent feature of it. In other words, the tissue exhibits what in other cases would be termed "sports." Such structural forecasts are well known and of frequent occurrence and as applied to the development of tissues no better example is afforded than that shown by the central strand of mosses, which is generally accepted as prophetic of the future vascular system

in the sporophyte. They serve to suggest that the law of mutation as proposed by De Vries finds expression in the evolution of internal structures as well as in the development of external forms. Such cases as *Sequoia gigantea*, which shows resin cysts in the wood of the first year and nowhere else, being replaced later by resin cells, appear to us to show that young and vigorous growth in general, and therefore the growth ring of the first year, constitutes a transitional zone within which many changes of structure wholly apart from the strictly normal may arise; and such a law would similarly be applicable to the wood of peduncles. This feature is manifested in the structure of the medullary ray, the character of the tracheids as exhibited in transverse section, the genesis of the bordered pits from spiral tracheids, and in all probability also in the formation of resin passages in Sequoia and Abies as noted by Jeffrey.

Changes of this nature are to be regarded as tendencies in development in the direction of higher types of structure whereby potentialities assume a more or less definite form. From this it may be assumed that the primary growth ring is a zone within which sporadic characters are common, but it is only in the later rings that the various anatomical characters become permanently developed and properly express the normal features of structure and development.

This view is justified not only by observed facts but also by analogy which shows that as plants ascend in the scale they exhibit sporadic characters or "sports" as tendencies toward the development of otherwise potential characters. As plants gain in complexity such tendencies become manifested not simply in alterations of external form but with respect to particular details of structure and development. We therefore find ourselves compelled to conclude that the development of resin cysts and resin passages from resin cells, and the occurrence of the latter in the Coniferales, shows that all of these structures are features in the development of higher types of plants, and it is difficult for us to accept the statement of Jeffrey that such resin passages represent primitive structures and are of the nature of survivals.

Returning to the question of the traumatic nature of the

resin cysts in Sequoia, Abies and Tsuga, which Jeffrey appears disposed to formulate as a general law, it is not clear to us how this can be made to harmonize with facts coming under our own observation. It has been shown that such resin cysts occur in one species of Sequoia, four species of Abies and one species of Tsuga, yet another species of which also shows them in a potential form. The same elements appear in each case, *viz.*:—

1. The cysts assume a definite form in distribution.

2. They always occupy a definite place in the scale of structural organization.

3. They are constant features of the same species.

4. They occur at frequent intervals in the same transverse section, showing them to be repeated at intervals of from one to several years.

It is exceedingly difficult to conceive how injuries could be inflicted upon particular species with such constancy, and in such a way as to produce uniform results in the production of resin cysts which occupy a definite place in the structural scale.

It is a well known fact in the physiology of plants, that conditions which induce a premature development of parts also bring about the conversion of potentialities into actualities, and under such circumstances the latter become evidences of a pathological condition. The swamp maple normally develops a brilliant foliage in the autumn, but it is not uncommon to find individual branches which have been injured, or even entire trees, which exhibit the characteristic autumnal foliage in midsummer, a condition which is correctly interpreted as pathological. Special conditions of nutrition, *e.g.*, an excess of mineral food elements, may similarly induce a premature development of the reproductive process. It has been shown by Richards that in cases of injury the rate of respiration is greatly increased, an alteration in functional activity which he rightly interprets as due to efforts directed toward the repair of injured parts. But this implies a local increase of nutritive materials and their application to a more intensive process of nutrition. Such features are well known in the case of all hypertrophies, and they must be similarly applicable to all forms of wounds, no matter what their origin, differing only in degree. We cannot

very well conceive of such profound functional disturbances without assuming a corresponding alteration in or development of those structures upon which the activities are dependent. The structural alterations may thus become characteristic, *local* features, and they may even represent the tangible expression of potentialities which are not manifested elsewhere in similar regions of the plant body. Furthermore, normal resin canals are invariable features of Larix, Pseudotsuga, Picea and Pinus. But Anderson (1, p. 29, etc.) has shown that in *Picea excelsa*, *Larix japonica* and *Pinus strobus* there is an enormous increase in the number of resin canals, arising through the unusual stimulus afforded by the operations of the mycelium of *Agaricus melleus*. With respect to *Abies firma* he also clearly shows that the general effect of the stimulus afforded by the parasite *Æcidium elatinum* (which gives rise to hexenbesen) is to produce a more perfectly organized form of the secretory reservoir than is present under normal conditions. To us, therefore, these facts offer a reasonable explanation of the appearance of resin cysts under conditions of injury, when they assume a pathological rôle, while they also serve to harmonize their occurrence under such circumstances with the general course of their evolution as already set forth.[1]

The results to which we are now brought are based entirely upon developmental phases in anatomical elements of the vascular cylinder. While our studies lead us to certain definite conclusions, we do not in any sense regard the latter as final, but only as affording one step in the solution of a question which must be viewed not only from the broader standpoint of more extended anatomical data, but from that of Physiology as well, although we feel disposed to insist that the final answer will be found to rest chiefly upon an anatomical basis. That there may be room for a different interpretation of the facts here recorded, is quite possible, since Dr. Jeffrey has recently permitted me to

[1] Since the above was written, Dr. Jeffrey has very kindly shown me several specimens which appear to afford strong evidence in support of his position, and in view of such facts the conclusions here stated are made with reserve until further evidence is at hand through the publication by him of studies now in progress.

examine the manuscript of an important contribution to our knowledge of the Abeitineæ, in which he brings out very significant facts suggestive of the idea that this group is of a much more primitive character than has hitherto been supposed, or than is indicated by our own studies. It is therefore of importance that final judgment should be suspended until the results of these various studies, as well as those of Coulter and Chamberlain, all directed to the same end but prosecuted along entirely distinct lines, can be brought together and co-ordinated. It is in this sense, therefore, that we offer the following.

SUMMARY AND GENERAL CONCLUSIONS.

In discussing the phylogeny of the higher Gymnosperms, three subordinate phyla must be taken into consideration in the following order:—(1) Cordaitales, (2) Ginkgoales, (3) Coniferales.

Regarding the Cordaitales as the most primitive gymnospermous stock of which we have present knowledge, it is possible to trace its origin to the Cycadofilices. The genera Lyginodendron, Heterangium, Calamopitys and Pityoxylon present many structural features which are common to all, and which not only establish their relation to the Cycadean line of descent, but they offer many suggestions of that course of development which is realized in the higher Coniferales. They therefore constitute the real starting point for two lines of descent, the first of which embraces the Cycadales. With this we have little or nothing to do at the present moment, beyond establishing its probable relation to the other gymnosperms. The second line emerges in a type of plants having characteristics distinctly allied to those of the Coniferæ, and it is this line of descent with which we are now chiefly concerned. It is now possible to define the origin of this phylum somewhat more exactly than Coulter has done (7 & 8), since there is good reason to believe that it emerges from the Cycadofilices through Poroxylon. Scott (52, p. 398) has already pointed out the relations of this genus to the Cycadofilices and the Cycadaceæ on the one hand, and to Cordaites on the other, so clearly as to remove the necessity for detailed

discussion at this time, beyond giving emphasis to one or two important structural relations. It has been noted that in *Calamopitys saturni*, the most primitive distribution of the bordered pits upon both the radial and tangential walls, is represented in the protoxylem structure. Such distribution, however, undergoes rapid modification whereby it is wholly limited to the radial walls in the secondary wood. A similar limitation appears in other, somewhat closely related genera, and it is fully expressed in Poroxylon where the multiseriate disposition and hexagonal form are typically preserved, though there is, at the same time, a tendency to segregation to such an extent that the pits sometimes become round. In this it is possible to notice the first indication of a character which, while infrequent, is nevertheless occasionally expressed among the Cordaitales, though it is generally characteristic of the related phyla Ginkgoales and Coniferales.

Among the Cordaitales there is but one genus (Cordaites) which we have heretofore been accustomed to associate with that phylum, and, so far as our present knowledge goes, it undoubtedly stands in the closest relations to Poroxylon. It is, however, improbable that the two were in any sense coterminous, and it is altogether probable that there may have been some one or more intermediate forms of which we have no present knowledge. Our present studies on the other hand, show clearly, that we must bring into this phylum two other genera of an obviously higher degree of development, but which have commonly been ranked with the Abietineæ and which, according to Eichler (11), occupy the highest position in the scale. This position is untenable upon anatomical grounds which give us reason to believe that Agathis and Araucaria (including, of course, Araucarioxylon) are not only inferior to the Coniferales as a whole, but that they are distinctly Cordaitean. Accepting this view, and the fact that Agathis is the inferior genus, the sequence would place Cordaites at the base and Araucaria at the top, with Walchia as the immediately ancestral form of the latter. This relation is not only natural, but it is justified on anatomical grounds.

The tendency to segregation of the bordered pits as exhibited by Poroxylon suggests the relation of this genus to others in

which such a feature is fully expressed, and it thereby forms the basal member of another series. From the opposite point of view, it has been shown that the occurrence of two-seriate pits in Pinus and others of the Coniferales, as well as in Ginkgo, points to a common origin for such genera in a type with multiseriate, hexagonal pits, and that both Agathis and Araucaria must likewise center in the same generalized form. This gradual convergence is justified on other grounds, and the genus Poroxylon among known forms most nearly fulfills the requirements of the case. We may therefore look upon it as lying between the Cycadofilices and all the higher gymnosperms, giving rise to two lines of descent, the first of which embraces the Cordaitales as already described, while the second shortly divides once more. This secondary division gives rise on the one side to the Ginkgoales, and on the other to the Coniferales. The anatomical data already discussed when viewed collectively show that the general sequence within the latter would be (1) the Taxoideæ, (2) the Taxodiinæ, (3) the Cupressineæ, (4) Abies, (5) Tsuga, (6) Pseudotsuga, (7) Larix, (8) Picea and (9) Pinus, of which one division (II) represents the highest type of development. The sequence of species for each genus cannot always be determined with a full measure of satisfaction, and these difficulties may possibly be made clear by reference to a particular case. The succession of the two species of Sequoia is difficult to determine on purely anatomical grounds, but the general tendency of the facts already recited is to give to *S. sempervirens* the more primitive position, a view which is sustained by its palæontological history.

The relations brought out in the foregoing studies, and the conclusions reached, may be made more obvious without the tedious method of a detailed discussion by reference to the accompanying table of anatomical data, which substantially summarizes all the results derived from the study of particular structures.

Data for Table of Anatomical Characters, in identical series.

1. Spiral tracheids.
2. Bordered pits in 1–3 rows.
3. Bordered pits in 1–2 rows.
4. Bordered pits in one row.
5. Pits on the tangential walls of the summer wood.
6. Lateral walls of the ray cells with bordered pits.
7. Uniseriate rays.
8. Terminal walls of the ray cells thin and entire.
9. Resin cells.
10. Terminal walls of the ray cells locally thickened.
11. Terminal walls of the ray cells strongly pitted.
12. Ray tracheids.
13. Resin passages.
14. Fusiform rays.
15. Thyloses in the resin passages.
16. Lateral walls of the ray cells with simple pits.
17. Ray cells of two kinds.

1. Resin cells scattering.
2. Resin cells zonate.
3. Resin cells grouped.
4. Resin cells on the outer face of the summer wood.
5. Ray tracheids marginal.
6. Ray tracheids interspersed.
7. Ray tracheids dentate.

A. Number of species.
B. Percentage value of genus.

TABLE OF ANATOMICAL CHARACTERS OF THE CORDAITALES, GINKGOALES AND CONIFERALES.

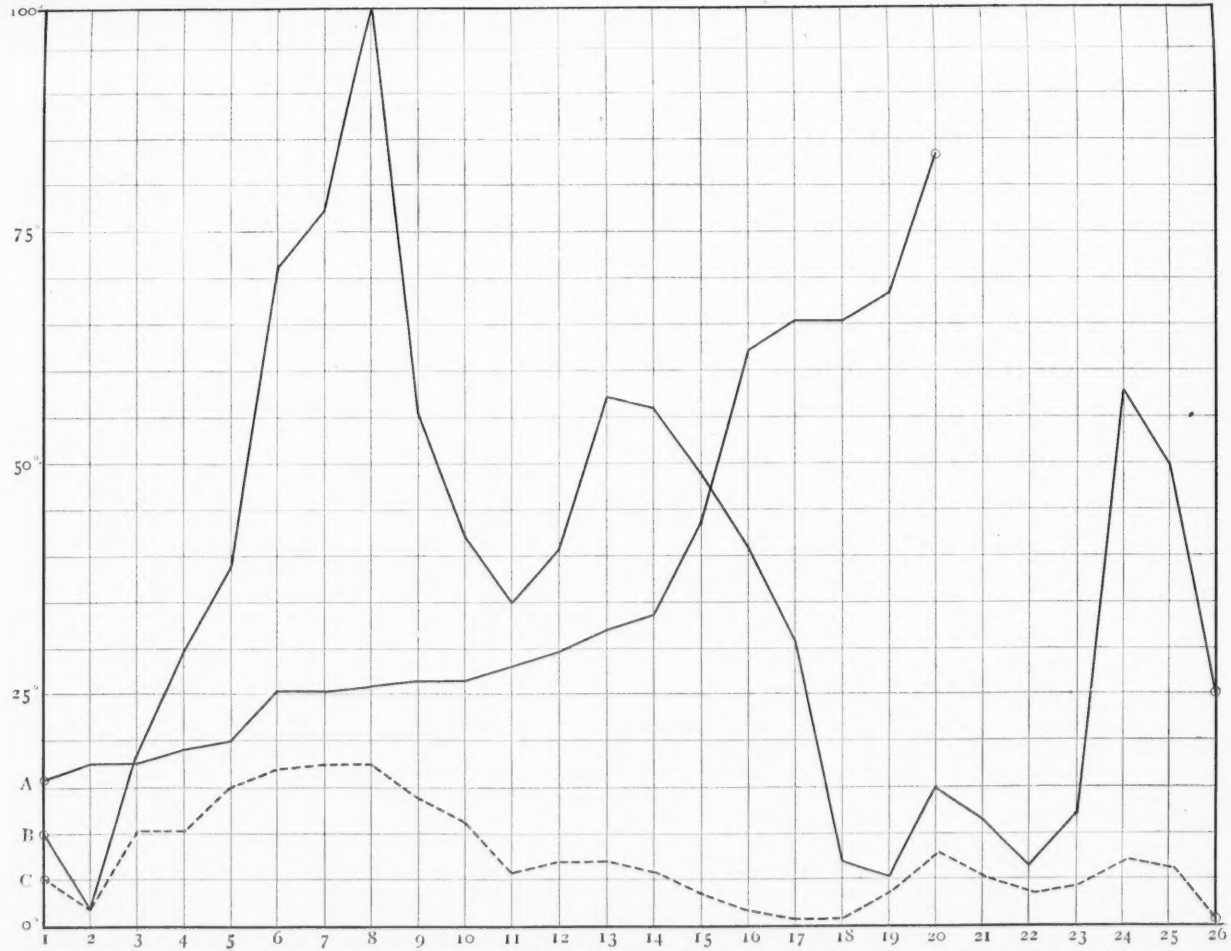
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
1 Agathis australis.	—	×			×	×	×	×																	1	16.
2 Araucaria cunninghami.	—	×			—	×	×	×										×							1	16.
excelsa.	—	—	×		—	×	×	×										×							3	17.7
bidwillii.	—	—	—	×	—	×	×	×										×	(0)						1	17.7
3 Ginkgo biloba.	—	—	×		×	×	×	×										(1)	×						1	26.4
4 Torreya taxifolia.	×	—	×		—	×	×	×										(1)	×						1	26.4
californica.	×	—	—	×+	×	×	×	×											×						3	28.2
nucifera.	×	—	—	×	—	×	×	×										×	(0)						1	25.4
5 Taxus floridana.	×	—	—	×—	×	×	×	×										×							1	25.4
canadensis.	×	—	—	×	×	×	×	×										×							1	25.9
brevifolia.	×	—	—	×	×	×	×	×										×							1	26.4
cuspidata.	×	—	—	×	×	×	×	×										×							1	26.4
6 Thujopsis dolabrata.	—	—	—	×	×	×	×	×	×									×							3	28.2
7 Cryptomeria japonica.	—	—	—	×	×	×	×—	×	×									×	(0)						4	19.9
8 Podocarpus macrophylla.	—	—	—	×	×	×	×	×	×									×							1	25.4
9 Taxodium distichum.	—	—	(1)	×	×	×	×	×	×									×							1	25.4
10 Libocedrus decurrens.	—	—	—	×+	×	×	×	×	×	(0)								×							1	25.9
11 Thuya gigantea.	—	—	—	×+	×	×	×	×	×									×							1	26.4
occidentalis.	—	—	—	×+	×	×	×	×	×									×							1	26.4
japonica.	—	—	—	×+	×	×	×	×	×									×							3	28.2
12 Sequoia sempervirens.	—	—	×		×	×	×	×	×			×						×	(0)						1	26.4
gigantea.	—	—	×		×	×	×	×	×				×—		×			×		×		×			2	29.7
13 Cupressus lawsoniana.	—	—	(1)	×	×	×	×	×	×									×							1	26.4
pisifera.	—	—	—	×+	×	×	×	×	×									×	×						9	32.0
obtusa.	—	—	—	×	×	×	×	×	×									×	×							
macrocarpa.	—	—	—	×+	×	×	×	—	×	×								×	(0)							
arizonica.	—	—	—	×	×	×	×	—	×	×								×		×						
macnabiana.	—	—	—	×	×	×	×	—	×	×									×							

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
13 Cupressus goveniana.	—	—	—	×	×	×	×	—	×	×								×								
thyoides.	—	—	(1)	×	×	×	×	—	×	×		×						×	(0)			×				
nootkatensis.	—	—	—	×	×	×	×	—	×	×		×						×	×			×				
14 Juniperus virginiana.	—	—	—	×+	×	×	×	—	×	×								—	×						11	33·4
nana.	—	—	—	×	×	×	×	—	×	×		(1)						—	×							
rigida.	—	—	—	×	×	×	×	—	×	×								—	×							
californica.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
utahensis.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
sabinoides.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
communis.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
sabina.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
pachyphloea.	—	—	—	×	×	×	×	—	×	—	×							(1)	×							
monosperma.	—	—	—	×	×	×	×	—	×	—	×								×							
occidentalis.	—	—	—	×	×	×	×	—	×	—	×								×							
15 Abies fraseri.	—	—	—	×+	×	×	×	—	—	—	×							—	—						11	43·5
lasiocarpa.	—	—	—	×	×	×	×	(1)	—	—	×							—	—							
veitchi.	—	—	—	×	×	×	×	—	—	—	×							—	—							
balsamea.	—	—	(1)	×	×	×	×	—	—	—	×	×						—	—	—	×	×				
magnifica.	—	—	—	×	×	×	×	—	×	(1)	×							—	—	—	×					
amabilis.	—	—	—	×+	×	×	×	—	×	—	×							—	—	—	×	×				
grandis.	—	—	—	×	×	×	×	—	×	(1)	×							—	—		×	×	×			
bracteata.	—	—	(1)	×	×	×	×	×	×	—	×		×—					—	—	×						
nobilis.	—	—	—	×+	×	×	×	—	×	—	×		×—					—	—	×						
concolor.	—	—	—	×	×	×	×	—	×	×	(1)		×—		×			—	—	×	×					
firma.	—	—	(1)	×	×	×	×	—	×	—	×		×—					—	—	×						
16 Tsuga canadensis.	—	—	×		×	×	×	—	×	—	×—	×						—	—	—	×	×	×		5	62.2
sieboldii.	—	—	—	×+	×	×	×	—	×	—	×	×						—	—	—	×	×	×			
caroliniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	×	×	×	×			
pattoniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	—	×	×	×	(0)		
mertensiana.	—	—	—	×	×	×	×	—	×	—	×	×	×—					—	—	×	×	×				

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
17 Pseudotsuga douglasii.	×	—	—	×+		×	×	—	×	—	×	×	×	×				—	—	—	—	×	(o)		2	65.2
macrocarpa.	×	—	—	×		×	×	—	×	×	×	×	×	×				—	—	—	—	×	(o)			
18 Larix occidentalis.	—	—	×		×	×	×	(1)	×	—	×	×	×	×				—	—	—	—	×	(o)		4	65.2
americana.	(1)	—	×		×	×	×	(1)	×	—	×	×	×	×				—	—	—	—	×	(o)			
lyallii.	—	—	—	×	×	×	×	—	×	—	×	×	×	×				—	—	—	—	×	(o)			
leptolepis.	—	—	—	+	—	×	×	—	×	—	×	×	×	×				—	—	—	—	×	(o)			
19 Picea breweriana.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)		10	68.5
rubra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
alba.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
engelmanni.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
jesoensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
polita.	—	—	—	+	—	×	×	—	—	×	×	×	×	×	(1)			—	—	—	—	×	(o)			
bicolor.	—	—	—	×	×	×	×	—	—	(1)	×	×	×	×	(1)			—	—	—	—	×	×			
pungens.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
nigra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×	×		—	—	—	—	×	(o)			
sitchensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×	×		—	—	—	—	×	(o)			
20 Pinus. Sec. I.	—	—	—	—	×	×	×	—	—	×	(1)	×	×	×	×	×	×	—	—	—	—	×	(o)		41	83.3
parryana.	—	—	—	—	×	×	×	—	—	(1)	×	×	×	×	×	×		—	—	—	—	×	(o)			
cembroides.	—	—	—	—	×	×	×	—	—	—	×	×	×	×	×	×		—	—	—	—	×	×			
monophylla.	—	—	—	—	×	×	×	—	—	—	×	×	×	×	×	×		—	—	—	—	×	(o)			
balfouriana.	—	—	—	—	×	×	×	(1)	—	—	×	×	×	×	×	×		—	—	—	—	×	(o)			
aristata.	—	—	—	—	×	×	×	(1)	—	—	×	×	×	×	×	×		—	—	—	—	×	(o)			
edulis.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	(o)			
lambertiana.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	×			
monticola.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	(o)			
flexilis.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	(o)			
reflexa.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	(o)			
strobus.	—	—	—	—	×	—	×	×	—	(1)	×	—	×	×	×	×		—	—	—	—	×	(o)			
parviflora.	—	—	—	—	×	—	×	×	—	—	—	—	×	×	×	×		—	—	—	—	×	(o)			
albicaulis.	—	—	—	—	×	—	×	×	—	—	—	—	×	×	×	×		—	—	—	—	×	(o)			

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
20 Pinus. Sec. II.																										
clausa.	—	—	×		—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
rigida.	—	—	—	×+	—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
serotina.	—	—	(1)	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
banksiana.	—	—	(1)	×	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
contorta.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
glabra.	—	—	—	×	—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
echinata.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
resinosa.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
koraiensis.	—	—	—	×+	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
thunbergii.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×		×		
densiflora.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
murrayana.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×		—	—	—	—	×	×	×		
arizonica.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
coulteri.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×		×		
tuberculata.	—	—	—	×+	—	(1)	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	×	×		
torreyana.	—	—	—	×+	—	—	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	(o)	×		
chihuahuana.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
jeffreyi.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
ponderosa.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
scopulorum.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
pungens.	—	—	—	×+	—	×	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
inops.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
muricata.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
insignis.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
sabiniana.	—	—	×		—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	(o)	×		
tæda.	(1)	—	×		—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
palustris.	—	—	×		—	—	×	×	—	—	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
cubensis.	—	—	×		—	—	×	×	—	×	×	×	×	×	×	×	×	—	—	—	—	×	×	×		

In preparing this table, the various anatomical features have been chosen with reference to (1) the constancy of their occurrence, (2) their structural prominence and (3) their obvious relation to diagnostic purposes. In their horizontal extension, an attempt has been made to arrange them in accordance with the law of frequency, as well as with reference to their relation to development, in such wise that while the spiral tracheid is assumed to be the most primitive type of the vascular structure, the presence of two kinds of cells in the medullary ray may be held to express the highest form of development. To the members of the series so constituted we may then assign arbitrary values in arithmetical sequence from one to seventeen; while those subordinate characters which are represented by different forms of distribution may be regarded as forming a second series similarly valued. Any primitive or other character which has become obliterated through development may be held to retain its original value with respect to the general course of such development, and it is always indicated by —. Vestigial structures occurring sporadically are designated by (1), and to them one half the value of the fully developed character is assigned. All normal features are designated by ×, which becomes × + when they show development toward the next higher form, or by × — when they show a definite tendency to degeneration. Sporadic characters which are obviously in the line of development are indicated by (o), but they are assigned only half values. On this basis it is possible to arrange a sequence of genera and species in such a manner as to exhibit a progressive development from the simple Agathis with a minimum of characteristics to the complex Pinus in which the greatest number of anatomical features are involved. Furthermore, through such a series it is possible to determine the relative position of the various genera by percentage values, and this gives the most valuable insight into the approximate relations of the various members within the general line of descent. Such relations are determined not only for each anatomical character, but for the collective characters. Reducing these facts to a graphic form, the accompanying curves will assist in making the relations more clear, especially in emphasizing the general course of develop-

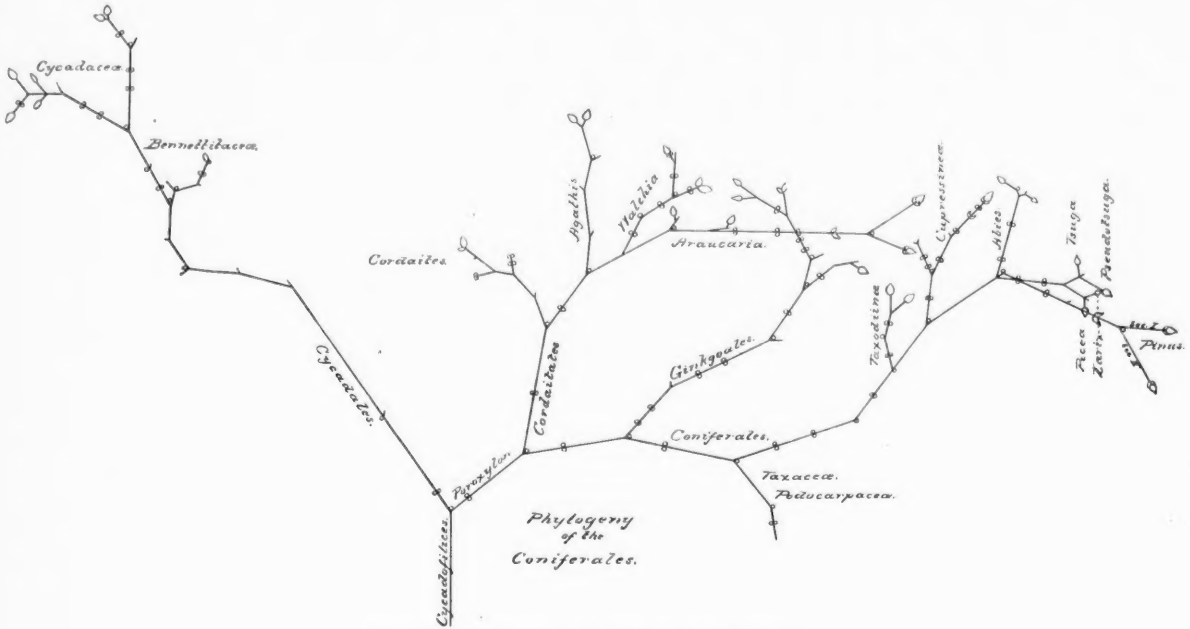


Curves for sequence of genera and frequency of anatomical characters, of the Cordaitales, Ginkgoales and Coniferales. A = Sequence of genera. B = Specific characters. C = Generic characters.

ment which in its final form is best expressed by a biological tree. A figure of this sort is difficult to construct, and there is no agreement among investigators as to the particular form it should take. While the figures in common use indicate a certain relationship in descent, they completely fail to convey any impression of the way in which the succession arises, and they furnish no indication of possible gaps. They therefore constitute a very poor working basis.

I have long been accustomed in teaching to compare the various lines of descent among plants with the branchings of a deliquescent tree, since it has always seemed reasonable to suppose that the laws which govern the branching of a limb, which give rise to all the varying forms of arrested development, and which thereby determine a particular modification of the figure which would otherwise result from unmodified growth, must be equally applicable to the general evolution of the higher forms of plants from a common ancestral type. In endeavoring to secure a natural growth which would best express all the conditions involved, a sympodium was first of all suggested, inasmuch as it conveys the idea of succession through lateral members in such a way as to indicate the direct line of descent. But sympodia as we usually know them fail to adequately express the idea of arrested development and suppression in their various forms. In the branching of *Acer platanoides* all the conditions appear to be met in a very satisfactory manner. The branch of the Norway maple, when of vigorous growth, is a monopodium, and it is obvious that such would not answer the object in view, since its most prominent feature would suggest the idea of a continuous series of coterminous members from which lateral members would arise at intervals. There is no evidence that any phylum represents such a series; on the contrary there is every reason to believe that such relations do not exist among the various groups of plants.

But in those branches of the Norway maple which exhibit slow growth various forms of arrested development are manifested. These take the form of atrophied buds, or of branches in all stages of development, and there thus arises a modified monopodium which eventually becomes, in many cases at least,



Diagrammatic representation of the Phylogeny of the Coniferales.

a true sympodium. In comparing this with the monopodial branch of vigorous growth, it appears that the alterations involve more than mere suppression. In the monopodium the average angle of divergence for the lateral members is 45.3°, while for the derived form it is 34.1°. The latter will be seen to completely fulfill all conditions with respect to the development of a phylum, even to indicating the position of missing members. Selecting from this such portion as may serve the requirements of the present case, we obtain the following figure which may be held to embody our final conclusions as to the general succession of the different gymnosperms, and from it we may gather that the highest representative — Pinus — is the terminal member in the main line of descent from the Cycadofilices through Poroxylon, while from such a central line both the Cordaitales and Ginkgoales have been given off as side lines. In the construction of this figure an attempt has been made to show all normally developed buds (o) and their relative dimensions; atrophied buds (o), the position of which is recognizable; and atrophied branches (/ —) which are still visible, but it is obvious that the figure does not show many members, all evidence of the former existence of which has completely disappeared.

The general results of these investigations serve to confirm in a very striking manner the probable monophyletic origin of the Gymnosperms as already expressed by Coulter (7), while they also show that the real transition ground, at least for all but the Cycadaceæ, was probably represented by Poroxylon as indicated by Scott (52).

LITERATURE.

ANDERSON, A. P.

(1.) Ueber abnorme Bildung von Harzbehaltern. München, 1896.

(2.) Comparative Anatomy of the Normal and Diseased Organs of Abies balsamea affected with Aecidium elatinum. Bot. Gaz., XXIV, p. 309–344. (2 pl.) 1897.

BENTHAM & HOOKER.

(3.) Genera Plantarum.

BRITTON, N. L., & BROWN, A.

(4.) An Illustrated Flora of the Northern United States and Canada. N. Y., 1896. Vol. I, 49–61.

CHAPMAN, A. W.

(5.) Flora of the Southern United States. 1884.

COOPER, J. G.

(6.) Smithsonian Report, 1858.

COULTER, J. M.

(7.) The Gymnosperms and the Seed Habit. Bot. Gaz., XXVI, 153–168. 1898.

COULTER, J. M., AND CHAMBERLAIN, C. J.

(8.) Morphology of the Spermatophytes. New York, 1901.

DE BARY, A.

(9.) Comparative Anatomy of the Phanerogams and Ferns. Oxford, 1887.

ENGELMANN, GEORGE.

(10.) Botanical Works. Cambridge, 1887.

EICHLER, A. E.

(11.) Naturlichen Pflanzenfamilien. II, 6 et seq.

ENGLER, A., AND PRANTL, K.

(12.) Naturlichen Pflanzenfamilien. II, 7–127.

ENGLER, A.

(13.) Naturlichen Pflanzenfamilien. II, 24 et seq.

ESSNER, B.

(14.) Diagnosticher Werth der Anzahl und Hohe der Markstrahlen bei den Coniferen. Bot. Centralbl., XII, 407, 1882.

FISCHER, H.

(15.) Ein Beitrag zur vergleichenden Anatomie des Markstrahlgewebes und der Jahrkichen Zuwachszonen im Holzkorper von Stamm, Wurzel und Aesten bei Pinus abies, L. Flora, vol. 68, p. 263 et seq. 1885.

GOEBEL, K.

(16.) Outlines of Classification and Special Morphology of Plants. Oxford. 1887.

GOEPPERT, H. R.

(17.) Fossilen Coniferen. Leiden, 1850.

GRAY, ASA.
(18.) Manual of Botany of the Northern United States. 1890.
HARTIG, GEORG LUDWIG.
(19.) Lehrbuch für Forster. Stuttgart, 1877.
HARTIG, R.
(20.) Das Holz der deutschen Nadelwaldbäume. Berlin, 1885.
HARTIG, THEODORE.
(21.) Anatomie und Physiologie der Holzpflanzen. Berlin, 1878.
HOOKER, SIR W. J.
(22.) Flora Boreali Americana. II, 165.
INDEX KEWENSIS.
(23.)
JEFFREY, E. C.
(24.) The Comparative Anatomy and Phylogeny of the Coniferales. Part I, The Genus Sequoia. Mem. Boston Soc. Nat. Hist. 1903.
KALM, P.
(25.) Travels in North America. II, 646.
KNOWLTON, F. H.
(26.) A Revision of the Genus Araucarioxylon of Kraus, with compiled descriptions and partial synonymy of the Species. Proc. U. S. Nat. Mus., XII, No. 784, 601–617. 1890.
MACOUN, JOHN.
(27.) Catalogue of Canadian Plants. Exogens. Geol. Surv. of Can. 1883.
(28.) Rept. Geol. Surv. Can., 1875–76. 211.
MASTERS, MAXWELL T.
(29.) Notes on the Genera of Taxaceae and Coniferae. Jn'l Linn Soc., XXX, I.
(30.) The Cypresses of Monterey. Garden & Forest, VII, 298.
MAYR, H.
(31.) Waldungen von Nordamerika. München, 1890.
MICHAUX, A.
(32.) Flora Boreali Americana. II, 1820.
MICHAUX, F. A.
(33.) The North American Sylva. III.
MULLER, N. J. C.
(34.) Atlas der Hölzstructur. Halle, 1888.
(35.) Botanische Untersuchungen. Heidelberg, 1872.
MURRAY, A.
(36.) Edinburgh New Phil. Jn'l. n. ser. I.
NÖRDLINGER, H.
(37.) Die Technischen Eigenschaften der Hölzer. Stuttgart, 1860.
NUTTALL, T.
(38.) The North American Sylva. III.

PENHALLOW, D. P.
(39.) Taxaceae and Coniferae. Trans. R. Soc. Can., II, iv, 33–57. 1896.
(40.) North American Species of Dadoxylon. Trans. R. Soc. Can., VI, iv, 51–79. 1900.
(41.) Notes on Tertiary Plants. Trans. R. Soc. Can., IX, iv, 33–95. 1903.
PIERCE, J. G.
(42.) Studies on the Coast Redwood. Cal. Acad. Sc., II, 83–106, 1901.
POTONIE, H.
(43.) Lehrbuch der Pflanzenpalæontologie. Berlin, 1899.
PRANTL, K.
(44.) Naturlichen Pflanzenfamilien. II, 33–40.
PURSH, F.
(45.) Flora Americana. 1816.
ROTH, FILIBERT.
(46.) Timber Pines of the Southern United States. U. S. Dept. of Agric., Div. of For., Bull. 13, 133–143.
RUSSOW, E.
(47.) Zur Kenntniss des Hölzes, insonderheit des Coniferenhölzes. Bot. Centralbl., XIII, 29. 1883.
SARGENT, C. S.
(48.) Forest Trees of North America. Tenth Census of the U. S., IX. 1880.
(49.) The Silva of North America. X, XI, XII. Boston, 1897.
SCHROEDER, J.
(50.) Holz der Coniferen. Dresden, 1872.
SCOTT, D. H.
(51.) The Anatomical Characters presented by the Peduncle of Cycadaceae. Ann. Bot., XI, 399–419. 1887.
(52.) Studies in Fossil Botany. London, 1900.
SEWARD, A. C. AND GOWAN, J.
(53.) The Maiden Hair Tree. (Ginkgo biloba, L.) Ann. Bot., XIV, 109–154.
WATSON, SERENO.
(54.) Botany of California. II. 1880.
WEISS, G. A.
(55.) Anatomie der Pflanzen. Wien, 1878.
WILLIAMSON, W. C.
(56.) On the Structure and Affinities of some Exogenous Stems from the Coal Measures. M. Mic. Jn'l, II, 66–72.
WITTSTEIN, G. C.
(57.) Organic Constituents of Plants, trans. by Baron F. von Mueller. Melbourne, 1878.
ZEILLER, R.
(58.) Eléments de Palæobotanique. Paris, 1900.

STUDIES ON THE PLANT CELL.—IV.

BRADLEY MOORE DAVIS.

SECTION III. HIGHLY SPECIALIZED PLANT CELLS AND THEIR PECULIARITIES (*Continued*).

4. The Spore Mother-cell.

THE spore mother-cell and its homologues the pollen mother-cell and certain embryo-sacs have furnished some of the most interesting subjects for cell studies in the plant kingdom. Sporogenesis in all plants above the thallophytes seems to be a period when nuclear structures are especially clearly differentiated and when the mechanism of mitosis reaches the highest degree of complexity. These intricate conditions are only equalled by processes in the development of the female gametophyte of some angiosperms, and during endosperm formation, also in the events of spermatogenesis and with the segmentation of the egg nucleus of certain gymnosperms.

Sporogenesis is one of the critical periods in the life history of a higher plant since it is the time when the asexual generation (sporophyte) passes over to the sexual (gametophyte). This provides certain important features such as the reduction phenomena concerned with chromosomes and greatly adds to the interest in these cells. These matters will receive special attention in Section V, but they must be borne in mind to appreciate fully the significance of many events of spore formation.

The general history of the spore mother-cell may be described as follows: It is the product of the last mitosis in the reproductive tissue called the archesporium. This mitosis always presents the number of chromosomes characteristic of the sporophyte which is double the number found in the gametophyte. Therefore the nucleus that passes into the spore mother-cell has the sporophyte number of chromosomes. Two

mitoses occur successively in the spore mother-cell in all forms. The first mitosis presents half the number of chromosomes found in the last nuclear division in the archesporium and is consequently the reduced or gametophyte number. The reduction of the chromosomes then takes place during the period of rest between the last mitosis in the archesporium and the first in the spore mother-cell. There are two mitoses in the spore mother-cell. In some forms these are exactly alike and present essentially the same characters as the usual typical mitoses of plants. But among the spermatophytes there are likely to be peculiarities in the arrangement and distribution of the chromosomes. In consequence the first mitosis may be heterotypic and the second homotypic in contrast to the normal typical conditions. The description and explanation of these characters will be reserved for the groups that illustrate them the best. They have nothing to do with qualitative reduction phenomena as was formerly supposed.

There is sometimes a well defined period of rest after the first mitosis with the formation of a wall between the two daughter nuclei, but frequently the second mitosis follows immediately after the first so that the spore mother-cell comes to contain four daughter nuclei. Cell walls may then be formed between these nuclei simultaneously so that the resultant spores are disposed in a radially symmetrical arrangement that is termed tripartite. These cell divisions are almost universally present in the spore mother-cell, the only exceptions being certain spermatophytes whose megaspore mother-cells develop directly into embryo sacs, the two mitoses (heterotypic and homotypic) being included within these structures and forming a part of the gametophyte history. Why the number of spores should generally be four is unexplained. There does not seem to be any physiological significance in the number or other reasons why it should not be more or less. Indeed it is somewhat variable in the spermatophytes for microspore or pollen mother-cells form two and three pollen grains in certain types and five, six and seven have been found in others, while much larger numbers have been occasionally reported. In no case is the microspore mother-cell known to develop directly into a pollen grain, al-

though the megaspore mother-cell regularly becomes an embryo sac in some forms (*e. g.*, Lilium). But an increasing number of observations indicate that the megaspore mother-cell generally develops two, three or four potential megaspores although normally only one of these becomes an embryo sac.

The interest in the protoplasmic activities of sporogenesis lie chiefly in the elaborate methods of spindle formation and mechanism of mitosis, in the organization and distribution of the chromosomes, in the functions and activities of the nucleolus, and in the organization of the cell plate and development of the cell wall. There is a very extensive literature on the spore mother-cell some of which, however, merely treats the broad features noted in studies of a general morphological character on the development of sporophylls or floral structures. We shall only attempt to consider the most important contributions, and for convenience will begin our treatment with the Hepaticæ and conclude with the spermatophytes where the conditions are the most complex.

The Hepaticæ or liverworts furnish some remarkable spore mother-cells, and are now the subject of considerable interest and some discussion. They were first brought conspicuously to the attention of botanists by a paper of Farmer ('94) on *Pallavicinia decipiens*. Farmer described a remarkable series of events in this type. The nucleus of the spore mother-cell became surrounded before division by dense protoplasm that extended into the four lobes of the cell in the form of a four-rayed star which he called a "quadripolar spindle." After its development four chromatic droplets appeared in the nucleus to indicate its approaching division. These chromatic droplets became four chromosomes which by division were doubled in number. The eight rod shaped chromosomes moved in pairs towards the four lobes of the spore mother-cell. There was a further division of each chromosome, making sixteen in all, and the four groups of four each passed simultaneously to the poles of the "quadripolar spindle" which persisted to the end. It should be noted that the striking peculiarities of Farmer's account lie in the division of the four primary chromosomes into sixteen, and in their simultaneous distribution through a "quadripolar

spindle" to form at once four daughter nuclei. These events are unparalleled, as far as the writer is aware, in the plant or animal kingdom, and consequently the account deserves especial attention. A four-rayed figure around the nucleus is not surprising because the spore mother-cell of the Jungermanniales is four lobed, and its centrally placed nucleus lies in a restricted area. But the simultaneous distribution of quadrupled chromosomes to form four daughter nuclei is a process whose establishment would be of fundamental significance. Farmer also described a centrosome at each pole of the "quadripolar spindle."

Farmer ('95*a*, *b*, and *c*) followed his paper on Pallavicinia with studies on other liverworts. He reported the "quadripolar spindle" in the early stages of mitosis in several of the Jungermanniales, but did not find the quadrupling and simultaneous distribution of the chromosomes as in Pallavicinia. The "quadripolar spindle" when present was a temporary structure replaced later by the bipolar spindles of two successive mitoses with a longer or shorter interval between. Farmer considers the "quadripolar spindle" of these forms as transitional between that of Pallavicinia and the normal bipolar spindle. The Ricciales, Marchantiales and Anthocerotales present two successive mitoses after the usual manner in the spore mother-cell.

The writer has described the events of sporogenesis in Pellia (one of the Jungermanniales) in a paper covering the nuclear activities at several periods in its life history (Davis, :01), and confirmed much of Farmer's account of the mitoses in this spore mother-cell. These are two in number and successive, with a very well defined resting period between the first and the second. There is a four-rayed figure present during the prophase of the first mitosis, and this seems to correspond to Farmer's "quadripolar spindle." The nucleus lying in the center of the four lobed spore mother-cell becomes invested by a kinoplasmic sheath which develops a fibrillar structure. Many of these fibrillae extend into the lobes of the spore mother-cell because the nucleus is confined to a narrow space in the constricted central region of the cell and the lobes offer the only possible relief for the crowded conditions. However, the four-rayed structure is not present when the chromosomes are ready for distribution,

but there is found instead one large, broad poled spindle. (See Fig. 5 *c*.) A cell wall is formed between the two daughter nuclei (Fig. 8 *d*) which divide again after a very short period of rest, the two spindles lying at right angles to one another. The poles of the spindles are rather blunt, and there are no centrosomes or centrospheres in either mitosis. The four-rayed structure of prophase must be regarded as preliminary to spindle formation because the chromosomes are not ready for distribution, and when that period arrives the structure has been replaced by the true spindle of the first mitosis. These facts led me to question Farmer's account of mitotic phenomena in Pallavicinia and his conception of the "quadripolar spindle," and I suggested that this structure might prove to be a phenomenon of prophase, a view to which Farmer (:01) has taken exception in a criticism of my results.

Recent investigations of Moore (:03) on Pallavicinia are flatly contradictory to the conclusions of Farmer for *Pallavicinia decipiens* and support my suggestions. Moore finds that there are two mitoses in the spore mother-cell of *Pallavicinia lyellii*, the second (Fig. 12 *c*, *d*) following immediately upon the first (Fig. 12 *b*), each with bipolar spindles and without centrosomes. The chromosomes, eight in number, appear in the usual way with each mitosis (Fig. 12 *c*, *d*). There is no "quadripolar spindle" in Farmer's sense, no quadrupling and simultaneous distribution of the chromosomes. The prophases preceding the first mitosis present a tetrahedral form as is shown in Fig. 12 *a*. This is accentuated by the fibrillae which gather at the points to make a four-rayed structure extending into the lobes of the spore mother-cell. This condition is identical with similar stages in Pellia and in other leafy liverworts, and is a feature to be expected from the fact that the spindle fibers develop chiefly or wholly externally to the nuclear membrane in a rather crowded region of the cell. The nucleus at this time is unquestionably in prophase as shown by the undifferentiated chromosomes and because this stage passes immediately into a bipolar spindle of the normal type (Fig. 12 *b*). It seems very probable that Farmer was mistaken in his conclusions for *Pallavicinia decipiens*, and that the mitoses in the spore mother-cell of this form

are not different in any essentials from those of other plants.

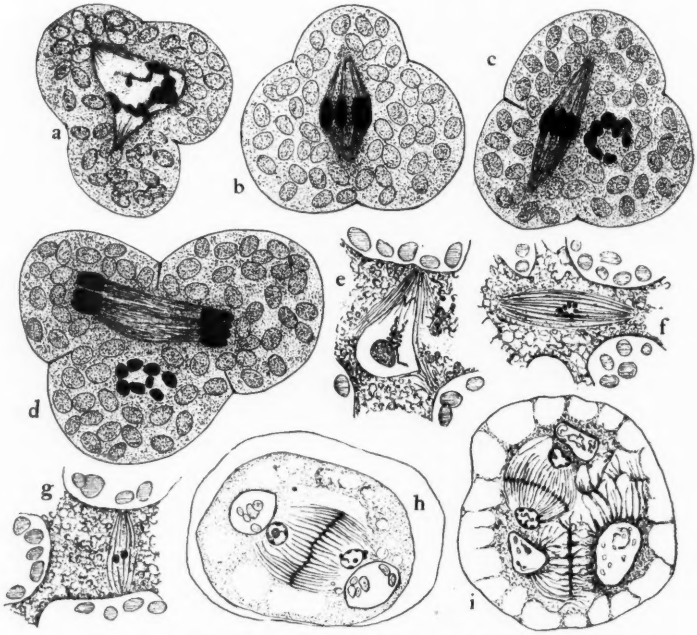


FIG. 12.— Spore mother-cells of Hepaticæ. *a, b, c, d, Pallavicinia lyellii. a*, Prophase; the fibrillæ gathered on four sides of the nucleus which has a tetrahedral form pointing into the four lobes of the spore mother-cell; the nuclear membrane has not yet broken down; similar stages of prophase were probably considered by Farmer as quadripolar spindles. *b*, metaphase of the first mitosis; the spindle in all respects a normal bipolar structure without centrospheres. *c*, Metaphase of the second mitosis; one spindle shown in side view, the other, almost perpendicular to the first, presents the eight chromosomes at the nuclear plate. *d*, anaphase of the second mitosis; one spindle viewed from the side, the other from one end shows the group of eight grand-daughter chromosomes. *e, f, g, anthoceros laevis, h, i*, a larger species from Italy. *e*, prophase; one pole of spindle developed. *f*, just after metaphase of the first mitosis; eight chromosomes; blunt poled spindle without centrospheres. *g*, metaphase of second mitosis; very small spindle. *h*, cell plate forming in the spindle between two nuclei. *i*, two nuclei at the side of their respective chromatophores and the cell plate between, after the second mitosis; a third chromatophore shown with strands of protoplasm connecting it with other regions of the cell. (*a, b, c, d*, after Moore, :03; *h, i*, after Van Hook, :00.)

The "quadripolar spindle" proves to be nothing more than a condition of prophase.

Besides Pellia and Pallavicinia, which are the most thoroughly studied of the lower liverworts, we know the processes of sporo-

genesis in the highest type, Anthoceros (Davis, '99). This form is exceedingly attractive for such investigations because the spore mother-cells may be found in all conditions upon the same sporophyte. However, the small size of the nuclei and spindles is a disadvantage. Just previous to the first mitosis the nucleus becomes surrounded by a mesh of delicate fibrillæ (kinoplasmic). Later the nucleus takes an angular form, and the fibrillæ are found conspicuously at the prominent poles (Fig. 12 *e*). The nuclear membrane breaks down and the fibers become arranged to form a bipolar spindle (Fig. 12 *f*) without centrosomes or centrospheres. There is a short period of rest after the first mitosis, but no wall is formed between the two daughter nuclei. The small spindles of the second mitosis (Fig. 12 *g*) are likewise bipolar. They lie at right angles to one another and the cell plates that are laid down determine, in part, the position of the walls that are formed between the four granddaughter nuclei and which divide the spore in a tripartite manner. These cell plates are very small (Fig. 12 *h* and *i*), but they have been observed in a favorable species of Anthoceros by Van Hook (:00). It is not clear how these plates become extended to the wall of the spore mother-cell unless (as suggested in Sec. II) their edges make use of planes of vacuoles when the protoplasm separates to develop the cleft between the four daughter cells. The poles of the spindles in Anthoceros are flattened and entirely free from structures that might be considered centrosomes.

Other interesting events of sporogenesis in Anthoceros are the division of the chromatophores and the nuclear condition termed synapsis. The young spore mother-cell contains a single large chromatophore. This increases greatly in size and becomes filled with starch grains. The chromatophore divides successively into two and then four portions which arrange themselves symmetrically in the cell with the nucleus in the center. The mitoses then follow and the four daughter nuclei are distributed, one for each chromatophore in the cell. This provision of four chromatophores long before the mitoses in the cell seems very remarkable (Davis, '99, p. 94 and 95). Synapsis is a condition very common in the nucleus of spore mother-cells before division. The chromatic material becomes gathered into a compact

mass besides the nucleolus. The significance of synapsis is not clear, but the subject will be discussed in Section VI. However, there is good evidence from Anthoceros that the phenomenon is a normal event and not an artefact, because synapsis is always found at a certain period of sporogenesis, and nuclei in neighboring spore mother-cells a little older or younger present their chromatic material with the usual arrangement (Davis, '99, p. 96 and 97).

To summarize the conditions in the spore mother-cells of the Hepaticæ, all conclusions, in the author's opinion, indicate: (1) That the spindles develop from a surrounding weft of fibrillæ without the assistance of centrosomes. (2) That the mitoses are always two in number and successive with the same number of chromosomes for each division. (3) That the cell walls may be formed successively as in Pellia and some other of the Jungermanniales or simultaneously, to give tetrahedral spores, as in Anthoceros, types of the Marchantiales and Ricciales, Pallavicinia and some companion forms in the Jungermanniales. It will be interesting to note the essential agreement in these matters between the Hepaticæ and the higher plants.

Nothing is known of the nuclear activities during sporogenesis in the other great division of the bryophytes, the mosses (Musci). The spore mother-cells in this group are always small and unattractive for cell studies but the Sphagnales appear to be rather the most promising for such investigations, which are greatly to be desired.

The pteridophytes have furnished some important contributions to our knowledge of the spore mother-cell. There is first the paper of Osterhout ('97) on spindle formation in Equisetum, which was one of a group of three contributions (Mottier, '97, Juel, '97) that did much to dispose of a then prevalent belief that the development of the spindle in higher plants was controlled by centrosomes. This investigation was followed by a study of Smith (:00) on spindle formation in Osmunda. Calkins ('97) and W. C. Stevens ('98*a*) considered especially the formation and reduction of chromosomes in several of the ferns, and arrived at contradictory conclusions. Strasburger (:00, p. 76 to 79) has reviewed these results in relation to studies of his own on Osmunda.

Osterhout's ('97) account of spindle formation in Equisetum is noteworthy. He found that the nucleus of the spore mother-cell became surrounded by a web of delicate fibrillæ, which, extending radially into the surrounding cytoplasm (Fig. 13 *a*), were later (Fig. 13 *b*) gathered into numerous pointed bundles or cones. After the dissolution of the nuclear membrane these

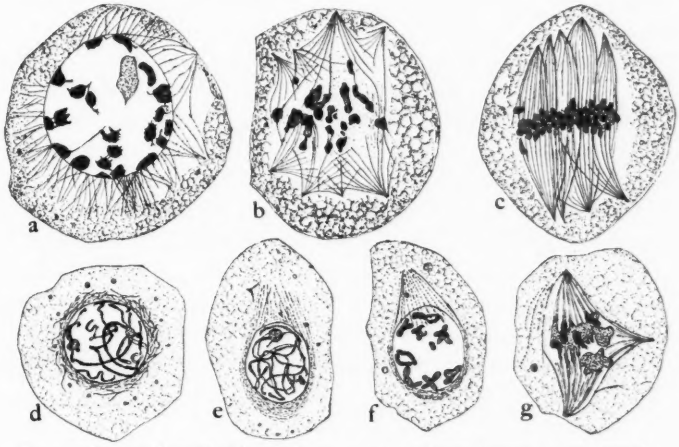


FIG. 13.— Spore mother-cells of Pteridophytes. *a*, *b*, *c*, *Equisetum limosum*. *a*, prophase of first mitosis; the radially disposed fibrillæ are gathering together into cones. *b*, prophase, older than *a*; the nuclear membrane has broken down and the fibrillæ have entered the nuclear cavity; the cones lie in two groups opposite one another. *c*, just before metaphase; the fibrillar cones are nearer together and the chromosomes have gathered to form the nuclear plate. *d*, *e*, *f*, *g*, *Osmunda regalis*. *d*, very early prophase of the first mitosis; nucleus in the spirem stage surrounded by a granular and fibrillar zone of kinoplasm. *e*, prophase, somewhat older than *d*; fibrillar kinoplasm showing polarity. *f*, still older; chromosomes formed; one pole of spindle developed. *g*, metaphase; a tri-polar spindle. (*a*, *b*, *c*, after Osterhout, '97; *d*, *e*, *f*, *g*, Smith, :00.)

cones arranged themselves side by side in two sets to form the spindle of metaphase (Fig. 13 *c*). The spindle is then from the outset multipolar, and even though some of the cones unite when they become grouped around a common axis, nevertheless the poles of the spindle at metaphase show their composite nature in the absence of a common focal point for the fibrillæ. There are no centrosomes at the poles and no reason for their presence at any stage in the process of spindle formation.

Smith's (:00) study of Osmunda presents an important confirmation of Osterhout's conclusions that the spindle in pteridо-

phytes developed without centrosomes, while illustrating a process of spindle formation along somewhat different lines. Smith distinguished a zone of kinoplasm around the nucleus previous to spindle formation. This zone became granular, and then the granules arranged themselves in rows to form fibrillæ (Fig. 13 *d*), which, however, did not extend into the cytoplasm radially, but lay generally parallel to one another, so that the spindle appeared bipolar from the beginning (Fig. 13 *e*). One pole of the spindle was generally formed considerably in advance of the other (Fig. 13 *f*). The fibers did not meet at a common point but over a broad area, and there were no centrosomes. There is, then, normally no multipolar stage in Osmunda, although tripolar spindles (Fig. 13 *g*) were occasionally found. During anaphase secondary fibers were put forth from the vicinity of the daughter nuclei and these met in the equatorial region of the cell. The spindle of the second mitosis was formed exactly as in the first. After this division the four granddaughter nuclei lay connected with one another by six spindles (two primary and four secondary). Cell plates were laid down in the equatorial regions of these spindles so that the protoplasm became divided simultaneously and symmetrically into tetrahedral spores.

The studies of Calkins ('97) and Stevens ('98*a*) were chiefly upon the division and distribution of the chromosomes in connection with reduction phenomena. Calkins believed that the processes of sporogenesis followed the same course as the maturation of sexual cells in animals, with a transverse division to give a qualitative reduction in Weismann's sense. Stevens disagreed with Calkins in several particulars, holding that the reduction was merely quantitative. Reduction phenomena in plants is now much better understood than at the time of these papers which dealt with plants much more difficult to study than some other forms (*e. g.*, types of the Liliaceæ). We shall consider the subject in Section V, but may state now that Calkins' conclusions have not been sustained.

Strasburger (:00) gives considerable attention to spindle formation in his well known review and critique of cytological literature. He proposes the following classification of spindles in higher plants which lack centrosomes. Those that pass

through multipolar stages and later become bipolar are called multipolar polyarch spindles. When the spindle has a well defined axis from the beginning, as is generally true of the cells in vegetative tissues of higher plants, it is termed multipolar diarch. Strasburger has shown that these types, while easily separated in the extremes, grade into one another so that the classification is not founded on distinctions of a very fundamental character. The spindle of Osmunda, for example, resembles a multipolar diarch, but its method of development is more closely related to that of other spindles in spore mother-cells (multipolar polyarchs) than to those of vegetative tissues.

The gymnosperms offer in Larix an excellent subject for studies on the formation of pollen, and this type has been treated in several important papers, notably by Belajeff ('94*b*), Strasburger ('95) and Allen (:03). Belajeff's contribution is important as the first investigation that considered the multipolar spindle as a preliminary stage in the development of the bipolar structure. Other authors, at this time and previous to his publication, had noted multipolar and tripolar spindles (Strasburger ('80) and ('88) in several forms), but the lily had received the greatest attention in this connection (Farmer ('93) and ('95*d*), Strasburger ('95), Sargent ('97) and Mottier ('97)). Mottier's investigation presented the first detailed account of spindle formation in this angiosperm and will be discussed presently.

Allen's (:03) paper on Larix includes one of the best discussions of the literature bearing on the subject of spindle formation that has yet appeared. He finds that the cytoplasm around the nucleus just previous to mitosis comes to contain a loose network of fibrillæ. Some of the fibers may be followed through the nuclear membrane and may be seen attached to chromatin bodies in the interior (Fig. 14 *a*). Later the cytoplasmic fibrillæ become arranged radially and extend from the nucleus even to the outer plasma membrane at the periphery of the pollen mother-cell. The radiating fibers are connected with one another by branches which indicate that the structure is in part an expanded condition of the original network, but the fibers also grow. The fibers now fold over so that they tend to lie parallel to

the surface of the nucleus and thus form a dense felt around the nuclear membrane. Presently the nuclear membrane which was before a definite film becomes wavy in outline and often granular in appearance. The nucleolus shows signs of dissolution and there is a marked increase in the number of intranuclear fibers, which are chiefly or wholly of nuclear origin. After the

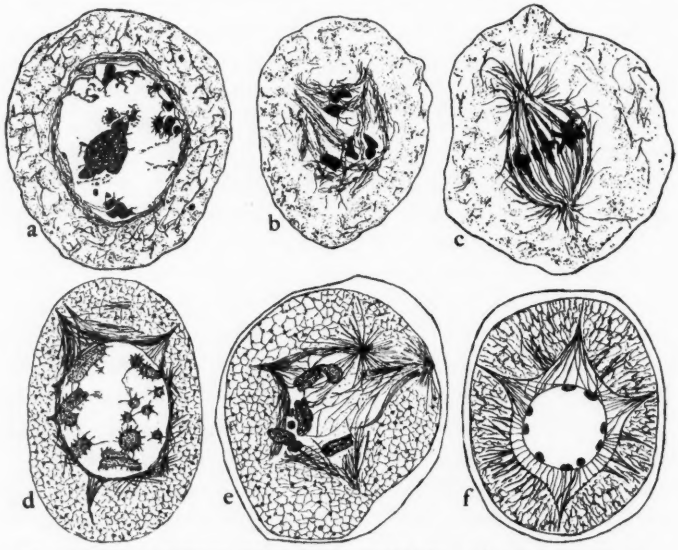


FIG. 14.— Pollen or microspore mother-cells of spermatophytes. *a, b, c, Larix europea. a*, prophase of first mitosis; kinoplasmic fibrillæ forming a felt around the nucleus. *b*, late prophase; the nuclear membrane has broken down and the interior space has become filled with fibrillæ which have gathered to form a multipolar spindle. *c*, metaphase; a completed spindle with polar radiations. *d, e, Lilium candidum. d*, prophase of first mitosis; the kinoplasmic fibrillæ have formed a net around the nucleus and are gathered into several cones which would have become poles of the spindle. *e*, late prophase; the nuclear membrane has disappeared and the fibril æ are entering the nuclear cavity; several cones of the fibrillæ constitute the multipolar spindle. *f, Agave Americana.* Prophase of the first mitosis; the spindle cones on the upper side have pushed through the special membrane around the nucleus. (*a, b, c*, after Allen, :03; *d, e*, Mottier, '97; *f*, Osterhout, :02.)

disappearance of the nuclear membrane some of the peripheral fibers push outward to form several cones of a multipolar figure (Fig. 14 *b*). The fibers attached to the chromosomes gather into bundles that extend towards these poles. Finally the bundles of fibers become more regular and straighten out so that they come to lie approximately parallel to one another, and thus

the multipolar structure, developing a distinct axis (Fig. 14 *c*), becomes bipolar (multipolar polyarch). There is no central body at the poles and no place for a centrosome in this developmental history.

The first detailed study of spindle formation in Angiosperms was, as before stated, that of Mottier ('97) which treated especially of Lilium, Podophyllum and Helleborus. This paper with one by Juel ('97) on Hemerocallis and Osterhout ('97) on Equisetum effectually disposed of previous views very generally held (Guignard, '91, followed by other authors), that spindle formation and mitotic phenomena in higher plants was involved with the activities of centrosomes or other kinoplasmic centers. Mottier found that the nucleus in the pollen mother-cell of the lily became invested just before mitosis with radiating fibers that shortly after increased in quantity to form a felted web around the structure. Some of the fibers gathered into cones (Fig. 14 *d*) which pointed towards the periphery of the cell so that there resulted, with the disappearance of the nuclear membrane and the entrance of the fibers into the nuclear cavity, a multipolar spindle (Fig. 14 *e*). The poles gradually came to lie parallel to one another in a common axis, some of them disappearing, so that the spindle generally became distinctly bipolar at metaphase (multipolar polyarch). Essentially the same history was repeated during the second mitosis in the lily.

From this time on there have been a succession of papers verifying the general conclusions of Mottier and Juel and extending these results to many other forms until now it seems to be well established that centrosomes are never present in the pollen mother-cell and that multipolar spindles, developed from felted stages and changing to bipolar spindles, may be expected in most if not all forms. Guignard ('97 and '98) described multipolar spindles in several types (Nymphæa, Nuphar, Limodendron, etc.), and while he believed that these poles were occupied by granules that sometimes fused to form typical centrosomes, nevertheless he admitted that the multipolar spindle might be formed independently of centrosomes.

The most important papers on spindle formation in Angiosperms following those of Mottier ('97 and '98) and Juel ('97)

have been Lawson ('98) on Cobea, W. C. Stevens ('98*b*) on Asclepias, Atkinson ('99) on Arisæma and Trillium, Duggar ('99) on Bignonia, Wiegand ('99) on Convallaria and Potamogeton, Gregoire ('99) on Lilium and Fritillaria, Guignard ('99) on Naias, Williams ('99) on Passiflora, Duggar (:00) on Symplocarpus and Peltandra, Lawson (:00) on Gladiolus, Byxbee (:00) on Lavatera, Andrews (:01) on Magnolia and Liriodendron, Schniewind-Thies (:01) on Galtonia and Osterhout (:02) on Agave.

Of the papers listed above several demand especial attention for the completeness of the studies on the early stages of spindle formation in the pollen mother-cell. Lawson ('98 and :00) found that the nuclei of Cobea and Gladiolus previous to mitosis were surrounded by a zone of granular kinoplasm which he named perikaryoplasm. This zone developed a felted envelope of fibrillæ from which projections extended to form the cones of a multipolar figure. The cones by fusing in two groups developed the bipolar spindles. The spindle fibers of Gladiolus are formed entirely from the perikaryoplasm, the nucleolus and linin apparently taking no part in the development of the spindle. The nucleolus remains intact until after the dissolution of the nuclear membrane when the spindle is practically completely organized. Miss Williams ('99) found for Passiflora that the nuclear cavity became filled with a network developed from the linin. The nuclear wall became also transformed into a mesh which connected the network from the linin with the surrounding cytoplasmic reticulum, thus forming a continuous system throughout the cell. The central region of this network, enclosed by a granular zone, developed a multipolar figure whose poles finally fused to form a bipolar spindle. The contrast between this type of spindle in which so much of the fibrous structure is derived from the linin and that of Gladiolus just described is very marked. A granular region outside of the fibrous network around the nucleus is much more conspicuous in Lavatera, described by Byxbee (:00), than in Passiflora. It forms in Lavatera a dense zone that suggests a gathering of nutritive material (deutoplasm). The fibrillæ are developed as a felt around the nuclear membrane and enter the nuclear cavity

with the breaking down of this structure. The fibers gather into projecting cones presenting a multipolar structure, and two of these, becoming more prominent, absorb the others and thus form a bipolar spindle.

One of the most recent studies on spindle formation is that of Osterhout (:02) on Agave. This investigation is of especial interest for the extensive experimentation in the technique of fixation. The author proposes a new terminology for the stages of mitosis that need not be presented here. Agave offers a striking peculiarity in the presence of a special membrane around the early stages of the spindle. The fibrillæ form inside of this membrane and finally push through it radially into the exterior cytoplasm where they gather into cones (Fig. 14 *f*). The cones separate into two opposite groups with a general parallel arrangement of the fibers and in this manner a bipolar spindle is formed.

It is becoming possible to make some general statements respecting the methods of spindle formation in the spore mother-cell. Just previous to prophase it is almost always possible to differentiate a region of kinoplasm around the nucleus. This zone has been found to be either granular, *e. g.*, Pellia, Anthoceros (Davis, '99 and :01), Osmunda (Smith, :00), Cobea and Gladiolus (Lawson, '98 and :00), or it presents the appearance of a fibrous reticulum, *e. g.*, Equisetum (Osterhout, '97), Larix (Allen, :03), Lilium (Mottier, '97 and '98), etc. The latter condition probably develops from the former by the arrangement of granules into fibers and the gradual expansion of a very close network thus formed into a coarser structure. The fibers in this reticulum sometimes surround the nucleus as with a heavy web. They later extend radially into the cytoplasm, partly by the expansion of the network and partly by their own growth and frequently take a radial arrangement. In some instances the spindle fibers are developed very largely within the nucleus from the linin (Passiflora, Williams, '99). They then become gathered into bundles or groups forming the cones which collectively constitute a multipolar figure that is often called a multipolar spindle. By the rearrangement of these cones somewhat parallel to one another, together with more or

less fusion, the multipolar structure becomes a bipolar spindle (multipolar polyarch) generally just previous to the period of metaphase. The formation of cell plates and the disappearance of the spindle fibers have been discussed in Section II under the title "Cleavage by cell plates."

Mention should be made of some irregularities in the division and distribution of the chromosomes that are conspicuous in certain spore mother-cells and which have been the cause of much discussion. The subject has especial reference to certain older views of the reduction phenomena in plants. Chromosomes split once longitudinally in all typical mitoses and the halves are drawn apart in a symmetrical manner which is very easily understood. This division is really determined by the longitudinal fission of the spirem thread. But appearances during the first nuclear division in the spore mother-cell of many forms have puzzled investigators for many years and have given rise to a number of interpretations. It seems to be pretty clearly established now that in these types there is a double longitudinal splitting of the chromosomes at the time of this mitosis. The first division takes place during prophase and the second follows closely after the first and is generally clearly seen at metaphase or during anaphase. Therefore the chromatic bodies which appear at the nuclear plate during the first mitosis are in reality divided or about to be divided into quarters and they separate after this mitosis as pairs of granddaughter chromosomes instead of simple daughter elements. These pairs are either firmly united at one end into a V or irregularly drawn out so that the bodies have very unusual and sometimes bizarre forms. Nuclear figures of this irregular appearance were originally described by Flemming for the first mitosis in the spermatocyte of Salamandra and named by him "heterotypic." These in the spore mother-cell of plants are of similar character and the designation "heterotypic" has been adopted by botanists for this condition. The pairs of chromosomes that enter the daughter nuclei after the first mitosis fuse end to end to form a spirem thread which breaks up again during the second mitosis, without longitudinal fission, into pairs of chromosomes which are believed to be identical with those that entered the nucleus after the first mitosis. Since there is

no longitudinal splitting of the spirem thread before the second division this mitosis differs from that of the "typical" mitoses of cells and is called "homotypic" to distinguish it on the one hand from the former and on the other from "heterotypic" divisions. Several illustrations of heterotypic and homotypic mitoses to be described presently are presented in Fig. 15, showing the peculiar V-shaped pairs of granddaughter chromosomes, characteristic of the first group. It is important to note that whatever the significance of this premature fission of the chromosomes before the second mitosis it is not of the nature of a qualitative reduction division in Weisman's sense. The details and significance of reduction phenomena will be considered in other connections (Section V). The topics discussed above have been recently studied and reviewed by Mottier (:03).

We have as yet said nothing of the megaspore mother-cell in Spermatophytes. An increasing number of investigations have clearly established the fact that the embryo-sac in many forms is one of a group of two, three or four cells, each of which is a potential megaspore because its nucleus contains the reduced number of chromosomes. We are accustomed to think of the well known conditions in the lily, where the megaspore mother-cell develops directly into the embryo-sac. But this type with some others (*e.g.*, Fritillaria, Tulipa, Erythronium, etc.) are the exceptions and present a very highly differentiated condition in which the usual developmental history is shortened in a very interesting manner, which will be described presently.

The embryo-sac arose undoubtedly as one of four megaspores developed after essentially the same manner as microspores or pollen grains, excepting that their arrangement was generally in a row, which is even true of some pollen grains (*e. g.*, Asclepias, Zostera). As stated above, an increasing number of investigations have established the row of four potential megaspores in a large number of forms in various groups. They may not always be distinguished by the form of the group, but their homologies are established by the mitoses that lead to their differentiation. Two mitoses are of course required to establish the group of four cells and both are identified by the reduced number of chromosomes. Some detailed studies on these mitoses have

established the fact for certain forms that the first is heterotypic and the second homotypic, exactly as in divisions of the micro-

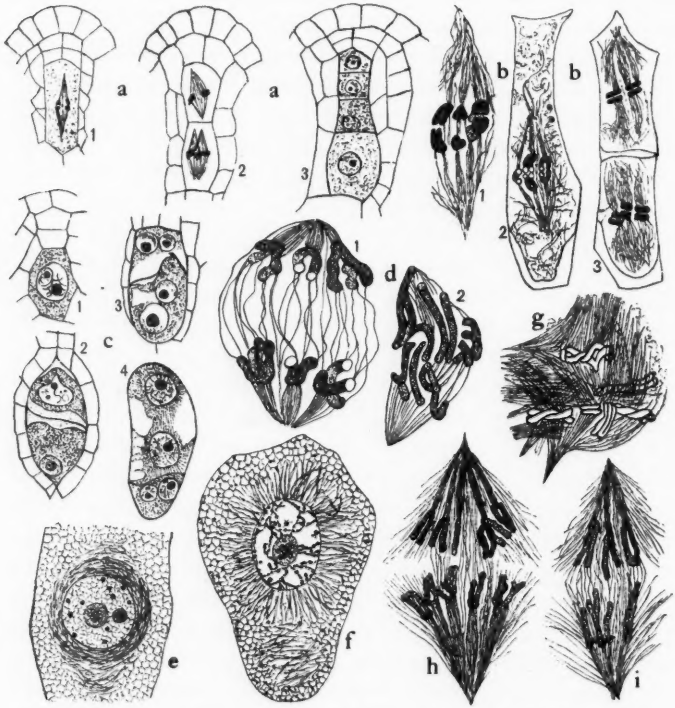


FIG. 15.—Embryo sac or megaspore mother-cell of spermatophytes. *a, b, Galtonia candicans.* *a1*, first mitosis in megaspore mother-cell. *a2*, second mitosis. *a3*, group of four megaspores. *b1* and *b2*, shortly after metaphase of the first mitosis (heterotypic). *b3*, metaphase of the second mitosis (homotypic). *c, d, Scilla Sibirica.* *c1*, megaspore mother-cell. *c2*, after the first mitosis. *c3*, after the second mitosis, the lower cell of the pair to become the embryo sac. *c4*, after the second mitosis, the upper cell of the pair to become the embryo sac. *d1*, anaphase of the first mitosis (heterotypic). *d2*, anaphase of the second mitosis (homotypic). *e, Lilium martagon*: portion of embryo sac mother-cell, nucleus surrounded by a felt of fibrillæ. *f, Lilium candidum*: embryo sac mother-cell, nucleus surrounded by radiating fibrillæ. *g, h, i, Lilium martagon.* *g*, late prophase of first mitosis in embryo sac mother-cell, a multipolar spindle. *h*, anaphase of first mitosis (heterotypic). *i*, anaphase of second mitosis (homotypic). (*a, b, c, d*, after Schniewind-Thies : 01 ; *e, f, g, h, i*, Mottier '97.)

spore or pollen mother-cells. Schniewind-Thies (:01) figures very completely the mitoses in Galtonia. The first mitosis in the megaspore mother-cell (Fig. 15*a*) is heterotypic because the

chromosomes (Fig. 15*b*, 1, 2) show clearly the V-shaped forms characteristic of this division. The second mitosis (Fig. 15 *b*, 3) is homotypic. The lowest cell of the group of four (Fig. 15 *a*, 3) becomes the embryo-sac and the mitoses that take place within it as the female gametophyte develops are all typical. This account illustrates a simple history in megaspore mother-cell development and is considered the first of three types in a classification proposed by Schniewind-Thies (:01).

The second type of development is one in which two megaspores are generally developed from a mother-cell and one of these becomes the functional embryo-sac. Schniewind-Thies presents an excellent illustration of this type in Scilla. The first mitosis in the megaspore mother-cell (Fig. 15 *c*) is heterotypic (Fig. 15 *d*, 1) and results in two cells (Fig. 15 *c*). The second mitosis in both cells is homotypic (Fig. 15 *d*, 2). Either the lower (Fig. 15 *c*, 3) or the upper (Fig. 15 *c*, 4) of the pair may become the embryo-sac. The embryo-sac then includes the homotypic or second mitosis within its development, making it the first nuclear division of the gametophyte history. The typical mitoses of the gametophyte begin with the second nuclear division in the embryo-sac. Three megaspores may be formed in such a group when the cell of the pair that does not become the embryo-sac divides again.

The third type of development is illustrated by several forms, of which the best known are Lilium (Mottier, '98 and :03) and Tulipa (Schniewind-Thies : 01). The lily has been much studied, but Mottier presents the most detailed account of spindle formation and the behavior of the chromosomes. He supports the observations of Schniewind-Thies, based upon the tulip, and her explanation of this type of development. The megaspore mother-cell of the lily and tulip develops directly into the embryo-sac. The first mitosis in this cell (Fig. 15 *h*) is heterotypic and the second (Fig. 15 *i*) homotypic. These divisions give the four-nucleate embryo-sac and one more mitosis presents the mature structure. This last is a typical mitosis, the only one found in the embryo-sac before the development of the endosperm and sporophyte embryo. Thus the two mitoses characteristic of the spore mother-cell are here included within the

embryo-sac and appropriated as a part of the gametophyte history.

We can see in these three types of embryo-sac development an evolutionary process of which the third stage is plainly derived from the simpler second and first, and is consequently a highly developed and very complex condition, far removed from primitive gametophyte structures among the angiosperms. The embryo-sacs of these forms (Lilium, Tulipa, Fritillaria, Erythronium, etc.) are probably the most complex spore mother-cells that we know. The studies of Schniewind-Thies and Mottier have been supported by other investigations, and more especially by the results of Ernst (:02) on *Paris quadrifolia* and *Trillium grandiflorum*, who followed the history of the heterotypic and homotypic mitoses in these forms in detail. They illustrate the second type of embryo-sac development in the classification of Schniewind-Thies.

Spindle formation in the embryo-sac mother-cell has not received as much attention as in the pollen mother-cell, probably because material of the latter structures may be obtained much more readily than the former. There have been numerous descriptions and figures of the spindles but few accounts in full of their development. Of the latter the investigation of Mottier ('98) on Lilium is the most complete. This paper was written at the time when the centrosome question was under discussion and served, with other papers on the spore mother-cell (Osterhont, '97, Juel, '97, Mottier, '97) to discredit the presence of these bodies in this structure. Mottier found that the nucleus of the embryo-sac became invested with a close network of fibrillæ (Fig. 15 *e*) from which fibers developed into the cytoplasm radiating from the nucleus in all directions (Fig. 15 *f*). With the dissolution of the nuclear membrane the fibrillæ entered the nuclear cavity, filling it with masses of fibers which gathered into cones to form a complicated multipolar spindle (Fig. 15 *g*). These cones later come together into two poles, but even in the mature spindle the fibrillæ are frequently in several groups at the poles. Essentially the same history is repeated in the second mitosis. A large number of later papers have described and figured multipolar spindles in embryo-sacs, con-

firming the conclusions of Mottier that these structures are developed here after the same methods as in the pollen mother-cell, from surrounding investments of fibrillæ and without centrosomes. Indeed the embryo-sac is remarkable for the quantity of the cytoplasmic fibrillæ present during its mitoses.

In concluding this account attention should be called to some forms whose microspore mother-cells were formerly supposed to omit the mitoses of sporogenesis and develop directly into pollen grains. These conditions were reported in Zostera, the Cyperaceæ, and the Asclepiadaceæ. However, Juel (:00) finds the two mitoses present in *Carex acuta*, although three of the nuclei break down and the cytoplasm is appropriated for the fourth to form a single pollen grain whose wall is developed from that of the mother cell. The history is very similar to the development of the megaspore in certain heterosporous pteridophytes (*e.g.*, Marsilia, Selaginella) and to the embryo-sac, which functions while its companion polential megaspores degenerate. The development of the pollen in the Asclepiadaceæ has been shown to be normal in the nuclear activities by several investigators (Frye, :01, Strasburger, :01, and Gagner, :02), the tetrad consisting of four pollen grains in a row, instead of the usual arrangement. In Zostera (Rosenberg, :01) there are longitudinal divisions of the very much elongated pollen mother-cell to give four extraordinary filiform pollen grains.

5. The Cœnocyte.

This remarkable type of cell has reached an extraordinarily high state of development in certain plants, notably among the Siphonales and the filamentous Phycomycetes (Mucorales, Saprolegniales and Peronosporales). Cœnocytes are multinucleate cells. The simplest types are developed by the limited division or fragmentation of a nucleus accompanied by an increase in the size of the cell but without extended growth. Excellent illustrations are found in the older cells of the red algæ, the internodal cells of the Characeæ and in old parenchyma cells of many higher plants.

A higher type of cœnocyte is presented when the multinucle-

ate cells show some definite activity resulting in extensive growth or peculiarity of form. Thus some laticiferous cœnocytes are branching tubes that grow for considerable distances among the cells of the tissues in which they are contained. The embryo-sac and the female gametophytes of Selaginella and Isœtes in the early stages of their development are interesting cœnocytes. Among the lower algæ there are numbers of cœnocytic forms (*e. g.*, Hydrodictyon, Cladophora) whose cells present very little change with age except an increase in size. Yet some of these conditions, especially those illustrated in the Cladophoraceæ, are probably related to the higher types of cœnocytes.

The best differentiated cœnocytes are found in the Siphonales, Mucorales, Saprolegniales and to a lesser extent among the Peronosporales and are especially well illustrated in a few aquatic forms, such as Monoblepharis and Myrioblepharis. The peculiarities of these forms lie in elaborate structures which result from the ability of the cœnocyte to respond to several directive stimuli in its growth. The most complicated responses and consequently the most highly differentiated morphology is shown among the Siphonales, where some very elaborate forms are found. In many types the plant body is clearly composed of root and shoot regions and in the highest expressions (*e. g.*, some species of Caulerpa) there are rhizoids, shoots and leaf-like structures presenting a remarkable degree of specialization. The behavior of the protoplasm in these most highly differentiated types of the Siphonales is known to us chiefly through studies of Noll and Klemm.

There is a very conspicuous layer of clear protoplasm next to the cell wall which constitutes an outer plasma membrane (hautschicht). This outer plasma membrane is stationary while the granular protoplasm within changes its position readily and frequently in different portions of the plant streaming in various directions. The nuclei are all situated in the granular cytoplasm so that they must shift their positions with its movements. Noll ('87) by a clever method of coloring the cell wall of living plants of Caulerpa was able to prove that the forward growth took place by the protoplasm extending beyond the old wall, thus adding new regions of cellulose to the old. He called this

method of growth a process of eruption in contrast to Nägeli's conception of growth by intussusception. Increase in thickness comes with the laying down of successive lamellæ inside the older wall and is consequently growth by apposition. Caulerpa is very favorable for such investigations and Noll's results greatly strengthen the theory that a cellulose wall results from the direct transformation of a plasma membrane in which carbohydrate molecules gradually replace those of albuminous material. Accordingly the cellulose wall is not strictly a secretion and its growth is not by the intercalation of new molecules among the old (intussusception) in a non-living membrane.

The wide space in the interior of the filaments of Caulerpa and some other members of the Siphonales is frequently crossed by cellulose bars at various angles. These are at first strands of protoplasm which become gradually filled with a carbohydrate material and finally solidified. Noll ('88*a*), while recognizing that these structures may have value in strengthening the filament, believes that they are also the paths of metabolic exchange between the interior regions of the protoplasm and the water outside the plant. They are surrounded by the plasma membrane which in consequence presents a much greater extent of surface to the water permeating the cell wall.

It is plain that because of the constant movement of the granular cytoplasm carrying with it the nuclei which change their position in the cell, the outer plasma membrane is the only portion of the protoplasm that can receive fixed stimuli for an extended period. Consequently Noll regards this membrane as the responsive or irritable region of the cell that reacts to the stimuli which largely or wholly direct growth. Some of these stimuli are well established. Thus it is light which directs the formation of leaves and shoots. The behavior of Caulerpa in relation to prominent stimuli (light, darkness, gravity, etc.) has been studied by Noll ('88*b*) and Klemm ('93). The latter author believes that the response is due to the presence of foods or other substances at certain points which make them especially sensitive to the external stimuli. Injuries to a filament of the Siphonales brings about an immediate flow of protoplasm to the wounded part (Klemm,' 94), after which the plasma membrane is quickly repaired and new portions of the wall laid down.

Mitotic phenomena in the Siphonales is known to us only through the investigations of Fairchild ('94) on Valonia. He found that nuclei in the same individual may divide directly or indirectly. The first process is one of simple fission, the latter takes place with the formation of an intranuclear spindle. Studies in sporogenesis and gametogenesis are very much to be desired in the Siphonales that we may understand the behavior of the nuclei at these periods. The author's recent studies of oögenesis in Vaucheria (Davis, :04*a*) have shown an interesting process of nuclear degeneration similar to that in the Saprolegniales and Peronosporales, and suggests some very interesting lines of investigation.

The protoplasmic structure in the hyphæ of the larger filamentous Phycomycetes, especially the Saprolegniales and Peronosporales, is undoubtedly much the same as in the Siphonales. But the absence of chlorophyll and the greater delicacy of the filaments makes it more difficult to recognize the different regions of the protoplasm. There is an outer plasma membrane inside of which the granular material slowly moves in protoplasmic currents that may sometimes be observed in rapidly growing tips. Delicate strands which are the paths of streaming currents are beautifully shown in developing sporangia of the molds and the oögonia of the Saprolegniales and Peronosporales. The nuclei are undoubtedly carried by the protoplasmic movements, sometimes collecting in cnnsiderable numbers in growing regions of the filaments which always contain much dense protoplasm.

Another type of cœnocyte, and in some respects the most remarkable, is the plasmodium of the Myxomycete. These structures are too well known to need description here. We shall only refer to them as they help to break down an old theory that the cœnocyte is a compound structure composed of many energids, represented by the nuclei, which coöperate to make up the whole. The plasmodium and the protoplasmic mass inside the cellulose tubes of the Siphonales and Phycomycetes agree in all essentials of structure and mode of growth. The forward growth of the plasmodium, as is also true of the Amœba, begins with the prolongation of the outer plasma mem-

brane (hautschicht, ectoplasm) into a process (pseudopodium) which advances and is followed immediately by an inflow of the granular cytoplasm. And the growth of the filaments of the Siphonales and higher Phycomycetes is a pushing forward of the outer plasma membrane followed by the granular protoplasm, but this growth is slow because the plasma membrane is at all times under the restraint of a cellulose envelope.

Mention should be made of the remarkable cœnocytic zoöspores well known in Vaucheria and also described by Thaxter ('95*b*), for the Phycomycete Myrioblepharis. In Vaucheria the entire contents of the sporangium becomes transformed into an immense multinucleate zoöspore, the cilia being distributed in pairs above the nuclei. In Myrioblepharis the contents of a sporangium usually forms four large multiciliate zoöspores.

These zoöspores of Vaucheria have often been called compound zoöspores, and the idea has been expressed that they stand for the coöperative union of many hundreds of zoöspores (energids) represented by the nuclei and their respective pairs of cilia. And this explanation of the zoöspore of Vaucheria is a part of a broad view, formerly very largely held, that the cœnocyte is an assemblage of energids (uninucleate masses of protoplasm) coöperating in a fused structure.

The theory of the coöperative association of energids in a cœnocyte (Sachs) has been very much modified. While the nucleus and some other organs of the cell, such as groups of cilia, plastids, etc., are homologous with the same structures in uninucleate cells nevertheless the behavior of the cœnocyte is not the same as a group of coöperating protoplasmic units. The cœnocyte reacts to the usual stimuli in precisely the same manner as a uninucleate cell, and must be regarded as physiologically presenting no peculiarities over the latter structure excepting those of an increased bulk of protoplasm demanding a greater number of nuclei for its metabolic processes. The most important contribution presented by the cœnocyte to our knowledge of the physiology of the cell is the establishment of the plasma membrane as the region of the protoplasm responsive to the stimuli that determine the form assumed in growth. The constant shifting of the nuclei and plastids in the movement of the

granular protoplasm eliminates them as structures immediately concerned with the form of a cell or organ thus limiting their functions more especially to metabolism.

6. The Cœnogamete.

The cœnogamete is a multinucleate sexual cell. The name was first applied by the author (Davis, :00, p. 307) to the remarkable multinucleate eggs of *Albugo bliti*, and the conception has been considerably extended since, as explained in his later writings on Saprolegnia (Davis, :03, p. 320–331) and on "The relationships of sexual organs in plants" (Davis, :04*b*). Stevens ('99) discovery of the multinucleate eggs of *Albugo bliti* opened a field of research that has been greatly extended in the past four years and which is likely to yield very important conclusions on the relationships and evolution of the Phycomycetes and Ascomycetes. Conditions similar to *Albugo bliti* were reported the following year by Harper, :00*b*, for Pyronema, and several later papers have described, with greater or less fullness, the structure and behavior of cœnogametes in some other Ascomycetes, types of the Peronosporales (species of Albugo) and in the Mucorales.

We shall not discuss the details of these investigations with their bearings upon the problems of phylogeny as this has become a very complicated subject and is treated elsewhere (Davis, :04 *a–b*), but merely describe the structure and behavior of cœnogametes so far as they are known to us.

Stevens and Harper both found that the multinucleate female cell of *Albugo bliti* and Pyronema was fertilized by the introduction of a large number of nuclei from the antheridium. These sexual nuclei paired off and fused, a male with a female, in the common mass of cytoplasm so that the fertilized cell finally contained a large number of fusion nuclei. A similar history was reported later by Stevens (:01), in *Albugo portulacae* and *Albugo tragopogonis*. These events have been so thoroughly studied that we know the processes of fertilization in the above forms as well perhaps as for any plant type.

The structure and especially the nuclear history of other

cœnogametes is less perfectly understood. The multinucleate character of the fusing gametes is well known, but the later distribution and fate of the sexual nuclei has not been followed, and it is by inference that we believe these cœnogametes to behave in essentially the same manner as those of Albugo and Pyronema.

Cœnogametes fall into two classes according as they involve all of the protoplasm contained within the mother-cell or only a portion of such protoplasm. The first group probably represents the simplest and most primitive conditions.

Cœnogametes of the first class are found in the Mucorales (Gruber : 01) and in the Gymnoasceæ (Dale, : 03). In these types the entire contents of the terminally formed sexual cells unite to produce the zygospore in the former group and the fertilized ascogonium in the latter, from which arises the system of ascogenous hyphæ.

Cœnogametes of the second class contain only a portion of the protoplasm in the mother-cell which is usually a terminal structure. The protoplasm that is not involved in the cœnogamete proper generally bears some important relation to the sexual element. Thus the periplasm of the Peronosporales assists in the formation of the wall of the oöspore and the conjugation tube of Pyronema becomes the path through which the contents of the antheridium enters the ascogonium. But in some forms the superfluous protoplasm is merely cut off from the cœnogamete as a sterile cell (Monascus). In Albugo and Pyronema the sterile and fertile portions of the protoplasm are so closely associated that the mother-cell really acts as a whole, very much as the simplest types of cœnogametes which shows the close relationships between the two. Moreover the antheridia of these forms are types of cœnogametes almost as simple as those of the molds or the Gymnoasceæ.

The cœnogamete is a type of sexual cell unknown in the animal kingdom and among plants is probably restricted to the Phycomycetes and Ascomycetes. The problems of its homologies and origin are very interesting.

The simplest types of cœnogametes (Mucorales and Gymnoasceæ) are cells situated at the ends of filaments in the same position as the sexual organs of the Siphonales. The mother-

cells of the more complicated cœnogametes (oögonia and antheridia) are also terminal cells. All of these sexual organs are multinucleate. In the Siphonales (Vaucheria excepted) all of the nuclei are functional gamete nuclei. This is also true of simplest types of cœnogametes, but in the more complicated forms (Albugo, Pyronema, etc.) large numbers of the nuclei degenerate or fail to function sexually in sterile accessory regions of the protoplasm. The same conditions of sexual degeneration are also found in the oögonia of Vaucheria (Davis, :04) and Saprolegnia (Davis, :03). The agreement of all of the structures mentioned above in structure and protoplasmic behavior seems to establish beyond question their common homology.

The problems of the origin of the cœnogametes are very difficult with the meager evidence at hand. The author believes that the simplest types have probably been derived from structures like the sexual organs of the isogamous Siphonales, which structures gave up the habits of forming uninucleate gametes and acting as cœnocytic units became multinucleate sexual elements. A physiological development very similar to such a change must have taken place in Peronospora and some species of Pythium when their conidia ceased forming zoöspores and took the habit of germinating directly by a tube. This view regards the cœnogamete as a cœnocyte derived from a protoplasmic structure that at one time produced a large number of independent sexual elements, represented in the cœnocyte by the numerous nuclei. Whether the higher types of cœnogametes (Albugo, Pyronema, etc.) have developed directly from the simpler forms or from levels of the heterogamous algæ, such as are illustrated by Vaucheria, are very complicated problems that cannot be treated here. They with other topics, mentioned above, have been considered in recent papers of the author (Davis, :03, ;04*a*, :04*b*). Cœnogametes are proving to be among the most interesting types of sexual cells in plants and research in this field is likely to prove very fruitful of results.

LITERATURE CITED FOR SECTION III. "THE PLANT CELL."

ALLEN.
:**03**. The early stages of spindle formation in the pollen mother-cell of Larix. Ann. of Bot. **17**, 281.

ANDREWS.
:**01**. Karyokinesis in Magnolia and Lirodendron. Bot. Centb. Beihefte **11**, 134.

ARNOLDI.
:**00***a*. Embryogenie von Cephalotaxus fortunei. Flora **87**, 46.

ARNOLDI.
:**00***b*. Was sind die Keimbläschen oder Hofmeisters–Körperchen in der Eizelle der Abietineen. Flora **87**, 194.

ATKINSON.
'**99**. Studies on reduction in plants. Bot. Gaz. **28**, 1.

BELAJEFF.
'**94***a*. Ueber Bau und Entwickelung der Spermatozoiden der Pflanzen. Flora **79**, 1.

BELAJEFF.
'**94***b*. Zur Kenntniss der Karyokinesis bei den Pflanzen. Flora **79**, 430.

BELAJEFF.
'**97***a*. Ueber den Nebenkern in spermatogenen Zellen und die Spermatogenese bei den Farnkrauter. Ber. d. deut. bot. Gesell. **15**, 337.

BELAJEFF.
'**97***b*. Ueber Spermatogenese bei den Schachthalmen. Ber. d. deut. bot. Gesell. **15**, 337.

BELAJEFF.
'**97***c*. Ueber die Aehnlichkeit einiger Erscheinungen in der Spermatogenese bei Thieren und Pflanzen. Ber. d. deut. bot. Gesell. **15**, 342.

BELAJEFF.
'**98**. Ueber die Cilienbildner in den spermatogenen Zellen. Ber. d. deut. bot. Gesell. **16**, 140.

BELAJEFF.
'**99**. Ueber die Centrosomen in den spermatogenen Zellen. Ber. d. deut. bot. Gesell. **17**, 199.

BLACKMAN.
'**98**. The cytological features of fertilization and related phenomena in Pinus silvestris L. Phil. Trans. Roy. Soc. **190**, 395.

BYXBEE.
:**00**. The development of the karyokinetic spindle in the pollen mother-cells of Lavatera. Proc. Cal. Acad. Sci. Bot. III, **2**, 63.

CALKINS.
'**97**. Chromatin reduction and tetrad-formation in Pteridophytes. Bull. Tor. Bot. Club, **24**, 101.
CAMPBELL.
'**88**. The development of Pilularia globulifera. Ann. of Bot. **2**, 233.
CAMPBELL.
'**91**. Contributions to the life history of Isoetes. Ann. of Bot. **5**, 231.
CAMPBELL.
'**92***a*. On the prothallium and embryo of Osmunda clatoniana, L. and O. cinnamomea, L. Ann. of Bot. **6**, 49.
CAMPBELL.
'**92***b*. On the prothallium and embryo of Marsilia vestita. Proc. Cal. Acad. Sci. II, **3**, 183.
CAMPBELL.
'**94**. Observations on the development of Marattia douglasii, Baker. Ann. of Bot. **8**, 1.
CHAMBERLAIN.
'**99**. Oögenesis in Pinus laricio. Bot. Gaz. **27**, 268.
COKER.
:**02**. Notes on the gametophytes and embryo of Podocarpus. Bot. Gaz. **33**, 89.
COKER.
:**03**. On the gametophytes and embryo of Taxodium. Bot. Gaz. **36**, 1 and 114.
DALE.
:**03**. Observations on the Gymnoasceae. Ann. of Bot. **17**, 571.
DANGEARD.
'**99**. Memoire sur les Chlamydomonadinees ou l'histoire d'une cellule. Le Bot. VI, 65.
DANGEARD.
'**01**. Etude sur la structure de la cellule et ses functions, Le Polytoma uvella. Le Bot. VIII, 5.
DAVIS.
'**99**. The spore mother-cell of Anthoceros. Bot. Gaz. **28**, 89.
DAVIS.
:**00**. The fertilization of Albugo candida. Bot. Gaz. **29**, 297.
DAVIS.
:**01**. Nuclear studies in Pellia. Ann. of Bot. **15**, 147.
DAVIS.
:**03**. Oögenesis in Saprolegnia. Bot. Gaz. **35**, 233 and 320.
DAVIS.
:**04***a*. Oögenesis in Vaucheria. Bot. Gaz. **38**, 81.
DAVIS.
:**04***b*. The relationships of sexual organs in plants. Bot. Gaz. **38**, 243.

DIXON.
'**94**. Fertilization of Pinus sylvestris. Ann. of Bot. **8**, 21.
DUGGAR.
'**99**. On the development of the pollen grain and embryo-sac in Bignonia venusta. Bull. Tor. Bot. Club, **26**, 89.
DUGGAR.
:**00**. Studies in the development of the pollen grain in Symplocarpus fœtidus and Peltandra undulata. Bot. Gaz. **29**, 81.
ERNST.
:**02**. Chromosomenreduction, Entwickelung des Embryosackes und Befruchtung bei Paris quadrifolia L. und Trillium grandiflorum Salisb. Flora, **91**, 1.
FAIRCHILD.
'**94**. Ein Beitrag zur Kenntniss der Kerntheilung bei Valonia utricularia. Ber. d. deut. bot. Gesell. **12**, 331.
FARMER.
'**93**. On nuclear division in the pollen mother-cells of Lilium martagon. Ann. of Bot. **8**, 392.
FARMER.
'**94**. Studies in Hepaticae: On Pallavicinia decipiens Mitten. Ann. of Bot. **8**, 35.
FARMER,
'**95***a*. Spore formation and karyokinesis in Hepaticæ. Ann. of Bot. **9**, 363.
FARMER.
95*b*. On spore formation and nuclear division in the Hepaticæ. Ann. of Bot. **9**, 469.
FARMER.
'**95***c*. Further investigations on spore formation in Fegatella conica. Ann. of Bot. **9**, 666.
FARMER.
'**95***d*. Ueber Kerntheilung in Lilium-antheren, besonders in Bezug auf die Centrosomenfrage. Flora, **80**, 56.
FARMER.
:**01**. The quadripolar spindle in the spore mother-cell of Pellia epiphylla. Ann. of Bot. **15**, 431.
FERGUSON.
:**01***b*. The development of the egg and fertilization in Pinus strobus. Ann. of Bot, **15**, 435.
FRYE.
:**01**. Development of the pollen in some Asclepiadaceæ. Bot. Gaz. **32**, 325.
GAGNER.
:**02**. The development of the pollinium and sperm cells in Asclepias Cornuti, Decaise. Ann. of Bot. **16**, 123.

GREGOIRE.
'99. Les cineses polliniques chez les Liliacées. La Cellule **16**, 325.
GRUBER.
:01. Ueber das Verhalten der Zellkerne in den Zygosporen von Sporodinia grandis Link. Ber. d. deut. bot. Gesell. **19**, 51.
GUIGNARD.
'91. Nouvelles études sur la fecondation. Ann. d. Sci. Nat. Bot. VII, **14**, 163.
GUIGNARD.
'97. Les centres cinétiques chez les végétaux. Ann. d. Sci. Nat. Bot. VIII, **6**, 177.
GUIGNARD.
'98. Centrosomes in Plants. Bot. Gaz. **25**, 158.
HARPER.
:00*b*. Sexual reproduction in Pyronema confluens and the morphology of the ascocarp. Ann. of Bot. **14**, 321.
HIRASE.
'94. Notes on the attractions-spheres in the pollen-cells of Ginko biloba. Bot. Mag. Tokyo **8**, 359.
HIRASE.
'97. Untersuchungen über das Verhalten des Pollens von Ginko biloba. Bot. Centb. **69**, 33.
HIRASE.
'98. Etude sur la fecondation et l'embryogenie du Ginko biloba. Jour. Coll. Sci. Imp. Tokyo, **12**, 103.
IKENO.
'98*a*. Zur Kenntniss des sogenanten centrosomähnlichen Körpers im Pollenschlauch der Cycadeen. Flora **85**, 15.
IKENO.
'98*b*. Untersuchungen über die Entwickelung der Geschlechtsorgane und den Vorgang der Befruchtung bei Cycas revoluta. Jahrb. f. wiss. Bot. **32**, 557.
IKENO.
:01. Contribution a l'etude de la fecondation chez le Ginko biloba. Ann. d. Sci. Nat. VIII, **13**, 305.
IKENO.
:03. Beiträge zur Kenntniss der pflanzlichen Spermatogenese: Die Spermatogenese von Marchantia polymorpha. Beitr. z. bot. Centb. **15**, 65.
JUEL.
'97. Die Kerntheilung in den Pollenmutterzellen von Hemerocallis fulva und die bei denselben auftretenden Unregelmassigkeiten. Jahrb. f. wiss. bot. **30**, 205.
JUEL.
:00. Beiträge zur Kenntniss der Tetradentheilung. Jahrb. f. wiss. Bot. **35**, 626.

KARSTEN.
'92. Beiträge zur Entwickelungsgeschichte der Gattung Gnetum. Bot. Zeit. **50**, 205, 221 and 237.

KARSTEN.
'93. Zur Entwickelungsgeschichte der Gattung Gnetum. Cohns Beit. z. Biol. d. Pflan. **6**, 337.

KLEBAHN.
'92. Die Befruchtung von Oedogonium boscii. Jahrb. f. wiss. Bot. **24**, 235.

KLEMM.
'93. Ueber Caulerpa prolifera. Flora, **77**, 460.

KLEMM.
'94. Ueber die Regenerationsvorgänge bei den Siphonaceen. Flora, **78**, 19.

LAND.
:02. A morphological study of Thuja. Bot. Gaz. **34**, 249.

LAWSON.
'98. Some observations on the development of the karyokinetic spindle in the pollen mother-cell of Cobea scandens. Proc. Cal. Acad. Sci. Bot. III. **1**, 169.

LAWSON.
:00. Origin of the cones of the multipolar spindle in Gladiolus. Bot. Gaz. **30**, 145.

LOTSY.
'99. Contributions to the life history of the genus Gnetum. Ann. Jar. Bot. Buiten. II, **1**, 46.

LYON.
:01. A study of the sporangia and gametophytes of Selaginella apus and Selaginella rupestris. Bot. Gaz. **32**, 131.

MIYAKE.
:03*a*. On the development of the sexual organs in Picea excelsa. Ann. of Bot. **17**, 351.

MIYAKE.
:03*b*. Contribution to the fertilization and embryogeny of Abies balsamea. Beitr. z. Bot. Centb. **14**, 134.

MOORE.
:03. The mitoses in the spore mother-cell of Pallavicinia. Bot. Gaz. **36**, 384.

MOTTIER.
'97. Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dikotylen und Monokotylen. Jahrb. f. wiss. Bot. **30**, 169.

MOTTIER.
'98. Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und die Vorgänge bei der Befruchtung. Jahrb. f. wiss. Bot. **31**, 125.

MOTTIER.
:**03**. The behavior of the chromosomes in the spore mother-cells of higher plants and the homologies of the pollen and embryo-sac mother-cell. Bot. Gaz. **35**, 250.

MURRILL.
:**00**. The development of the archegonium and fertilization in the hemlock spruce (Tsuga Canadensis Carr.) Ann. of Bot. **14**, 583.

NOLL.
'**87**. Experimentelle Untersuchungen uber das Wachsthum der Zellmembran. Abhand. d. Senc Kenberg. naturf. Gesell. **15**, 101.

NOLL.
'**88***a*. Ueber die Function der Zellstoffasern der Caulerpa prolifera. Arbeit. a. d. bot. Inst. Würz. **3**, 459.

NOLL.
'**88***b*. Ueber den Einfluss der Lage auf die morphologische Ausbildung einiger Siphoneen. Arbeit a. d. bot. Inst. Wurz. **3**, 466.

OLTMANNS.
'**95**. Ueber die Entwickelung die Sexualorgane be Vaucheria. Flora, **80**, 388.

OLTMANNS.
'**98**. Die Entwickelung der Sexualorgane bei Coleochæte pulvinata. Flora, **85**, 1.

OSTERHOUT.
'**97**. Ueber Entstehung der karyokinetischen Spindel bei Equisetum. Jahrb. f. wiss. Bot. **30**, 159.

OSTERHOUT.
:**02**. Spindle formation in Agave. Proc. Cal. Acad. Sci. Bot. **2**, 255.

PRINGSHEIM.
'**58**. Morphologie der Oedogonieen. Jahrb. f wiss. Bot. **1**, 1.

PRINGSHEIM.
'**60**. Die Coleochætaceen. Jahrb. f. wiss. Bot. **2**, 1.

ROSENBERG.
:**01**. Ueber die Pollenbildung von Zostera. Med. Stosk. Hogsk. Bot. Inst. 21.

SARGANTS.
'**97**. The formation of sexual nuclei in Lilium martagon: Spermatogenesis. Ann. of Bot. **11**, 187.

SCHIMPER.
'**85**. Untersuchungen über die Chlorophyllkörper und die in ihnen homologen Gebilde. Jahrb. f. wiss. Bot. **16**, 3.

SCHNIEWIND-THIES.
:**01**. Die Reduction der Chromosomenzahl und die ihr folgenden Kerntheilungen in der Embryosackmutterzellen der Angiospermen. Jena.

SHAW.
'**98***a*. The fertilization of Onoclea. Ann. of Bot. **12**, 261.

SHAW.
'98*b*. Ueber die Blepharoplasten bei Onoclea und Marsilia. Ber. d. deut. bot. Gesell. **16**, 177.

SMITH.
:00. The achromatic spindle in the spore mother-cell of Osmunda regalis. Bot. Zeit. **30**, 361.

STEVENS, F. L.
'99. The compound oösphere of Albugo bliti. Bot. Gaz. **28**, 149.

STEVENS, F. L.
:01*b*. Gametogenesis and fertilization in Albugo. Bot. Gaz. **32**, 77.

STEVENS, W. C.
'98*a*. Ueber Chromosomtheilung bei der Sporenbildung der Farne. Ber. d. deut. bot. Gesell. **16**, 261.

STEVENS, W. C.
'98*b*. The behavior of kinoplasm and the nucleolus in the division of the pollen mother-cells of Asclepias Cornuti. Kansas Univ. Quart. **7**. 77.

STRASBURGER.
'72. Die Coniferen und die Gnetaceen.

STRASBURGER.
'80. Zellbildung und Zelltheilung. Jena.

STRASBURGER.
'88. Ueber Kern-und Zelltheilung im Pflanzenreich, nebst einem Anhang über Befruchtung. Hist. Beitr. **1**.

STRASBURGER.
'92. Schwarmsporen, Gameten, pflanzlichen Spermatozoiden. Hist. Beitr. 4, **49**.

STRASBURGER.
'95. Karyokinetische Probleme. Jahrb. f. wiss. Bot. **28**, 151.

STRASBURGER.
:00. Ueber Reductionstheilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich. Hist. Beitr. **6**.

STRASBURGER.
:01. Einige Bemerkungen zu der Pollenbildung bei Asclepias. Ber. d. deut. bot. Gesell. **19**, 450.

THAXTER.
'95*a*. New or peculiar aquatic fungi: Monoblepharis. Bot. Gaz. **20**, 433.

THAXTER.
'95*b*. New or peculiar aquatic fungi: 2, Gonapodya and Myrioblepharis. Bot. Gaz. **20**, 477.

THOM.
'99. The process of fertilization in Aspidium and Adiantum. Trans. Acad. Sci. St. Louis, **9**, 285.

TIMBERLAKE.
:**02**. Development and structure of the swarmspores of Hydrodictyon. Trans. Wis. Acad. Sci. Arts and Letters **13**, 486.
VAN HOOK.
:**00**. Notes on the division of the cell and nucleus in liverworts. Bot. Gaz. **30**, 394.
WAGER.
'**99**. On the eye-spot and flagellum in Euglena viridis. Jour. Linn. Soc. **27**, 463.
WEBBER.
'**97***a*. Peculiar structures occurring in the pollen tube of Zamia. Bot. Gaz. **23**, 453.
WEBBER.
'**97***b*. The development of the antherozoids of Zamia. Bot. Gaz. **24**, 16.
WEBBER.
97*c*. Notes on the fecundation of Zamia and the pollen tube apparatus of Ginko. Bot. Gaz. **24**, 225.
WEBBER.
:**01**. Spermatogenesis and fecundation of Zamia. Bu. Plant Ind. U. S. Dept. Agri. Bull. **2**.
WIEGAND.
'**99**. The development of the microsporangium and microspores in Convallaria and Potomogeton. Bot. Gaz. **28**, 328.
WILLIAMS, CLARA I.
'**99**. The origin of the karyokinetic spindle in Passiflora cœrulea. Proc. Cal. Acad. Sci. Bot. **1**, 189.
WILSON.
:**00**. The cell in development and inheritance. New York.
ZACHARIAS.
'**87**. Beiträge zur Kenntniss des Zellkerns und der Sexualzellen. Bot. Zeit. **45**, 345.
ZIMMERMANN.
'**93**, '**94**. Sammel-Referate aus dem Gesammtgebiete der Zellenlehre. Beihf. z. bot. Centb. **3**, 206, 321, 401 (1893), **4**, 81, 161, 321 (1894).
ZIMMERMANN.
'**96**. Die Morphologie und Physiologie des Pflanzlichen Zellkernes. Jena.

(*To be continued.*)

THE AFFINITIES OF THE OPHIOGLOSSACEÆ AND MARSILIACEÆ.

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THE last ten years have been notable for many important contributions to our knowledge of the pteridophytes, due in part to a more exact investigation of many forms already studied, but still more to a critical study of tropical types, which hitherto have been studied more or less superficially, owing to the difficulty of procuring suitable materials for complete investigations. The fossil forms have also yielded much important material for a better understanding of the affinities of some of the living ones.

The work has covered a wide field and comprises very valuable additions to our knowledge of the anatomy and development of many interesting types which were but imperfectly known before. These investigations have added materially to the data available for a critical comparison of the different groups, and we are in a much better position than ever before to understand the affinities of some of the more puzzling types of pteridophytes. It must be admitted, however, that the conclusions of botanists in regard to the relationships of certain groups are by no means entirely in accord.

There are two orders of ferns about whose relationships there has been a good deal of controversy, and it is the bearing of some of the recent investigations upon these relationships to which the writer would direct attention. The two orders referred to are the Ophioglossaceæ and the Hydropteridineæ, especially the Marsiliaceæ.

THE OPHIOGLOSSACEÆ.

The Ophioglossaceæ constitute a very natural family of fern-like plants, evidently closely related among themselves, but

whose affinities to the other pteridophytes have been much discussed. They are generally considered to belong to the Filicineæ, or ferns with which they agree in their general structure. The writer has expressed the opinion that the sporangium of Ophioglossum represents the lowest type found in the fern series. This conclusion is based upon the structure of the living forms, as the Ophioglossaceæ are almost unknown in a fossil condition, perhaps owing to the soft tissues which characterize them. These would hardly be preserved as fossils except under the most favorable conditions.

As is well known, the Ophioglossaceæ differ from the typical ferns in the position of the sporangia, which are borne upon a peculiar structure (sporangiophore) arising from the inner surface of the leaf, either directly from the lamina or from the petiole. The sporangiophore may be a simple spike with two rows of large sporangia scarcely projecting at all, or it may be much branched and the numerous sporangia quite distinct and even stalked. (Campbell, *Mosses and Ferns*, p. 296.) The former structure occurs in Ophioglossum, the latter in Botrychium and Helminthostachys. The simpler species of Botrychium, such as *Botrychium simplex* and *Botrychium lunaria*, form a transition between the type of Ophioglossum and the larger species of Botrychium and Helminthostachys, in which both the sterile and fertile leaf segments are much branched, and the free sporangia bear a certain resemblance to those of Osmunda or Angiopteris. It is possible that the latter types, or at any rate Osmunda, may have arisen from forms like Botrychium or Helminthostachys, through which they would be connected with the more primitive type of sporangium found in Ophioglossum.

Much the most important recent work upon the sporangia of these puzzling forms is that of Bower ("Studies in the Morphology of Spore-Producing Members"; *Phil. Trans.*, 1894–1903, 185–196), whose views as to the relationship of the Ophioglossaceæ differ radically from those of most students of the pteridophytes. He considers the whole spike of Ophioglossum as the equivalent of a single sporangium of Lycopodium, produced by growth and septation from an originally unilocular structure. He is not inclined to admit any direct relationship

between the Ophioglossaceæ and the true ferns, and thinks they are probably more nearly related — although very remotely — to the lycopods. In his most recent work (*loc. cit.* No. V, p. 253), however, he recognizes the importance of the decidedly fern-like character of the gametophyte and recedes somewhat from the extreme views expressed in the earlier paper. He seems still unwilling, however, to give up the homology between the sporophyll in Ophioglossum and Lycopodium. It is held that all the pteridophytes are reducible to a common strobiloid type, which is most clearly seen in the lycopods and Equisetaceæ, but which is believed to be recognizable in the ferns as well. With this view the writer has been unable to agree.

Bower thinks it inconceivable that a large-leaved type could originate directly from any conceivable form of bryophyte sporogonium, and therefore concludes that all the primitive pteridophytes must have been microphyllous. To the writer there seems to be no greater difficulty in assuming that a single leaf-like organ may have been developed at the base of the sporogonium (*Mosses and Ferns*, p. 515) than that a series of small leaves should be developed as eruptions from its surface. Why both forms may not have been developed quite independently is not clear, either from the evidence of comparative morphology, or from the fossil record. That a special assimilative structure, remotely comparable to a leaf, may originate from the base of the sporogonium is shown in many mosses, where the apophysis is of this nature. In certain species of Splachnum the apophysis assumes a relatively very large size, and is expanded into a disc which might almost be compared to a perfoliate leaf. Of course there is no question of a direct homology between the apophysis of a moss and the leaf of a vascular plant, but the fact is patent that the sporogonium of a moss may give rise to a special assimilating organ, and it is therefore quite conceivable that the progenitor of the large-leaved ferns may have arisen from some bryophytic type by an analogous formation of a special organ which became a true leaf subtending a sporogenous structure much as is actually seen in Ophioglossum.

That the Ophioglossaceæ represent an ascending series, as Professor Bower (Bower, *loc. cit.* No. 5, p. 233) believes, is

extremely probable; but that the lowest members of the series are to be connected with forms in any way like the Lycopodiaceæ appears to the writer exceedingly doubtful. The direct origin of a type like Ophioglossum from an Anthoceros-like prototype has been considered at length elsewhere (Campbell, — *loc. cit.*, p. 515) and will not be discussed further here.[1]

The numerous structural resemblances in both gametophyte and sporophyte between the Ophioglossaceæ and Marattiaceæ are too great to be passed over, and indicate a genuine relationship between the two. It seems to the writer that the importance of these obvious resemblances has been rather minimized by some recent authors, and it may be just as well to call attention afresh to some of the most striking ones.

Our knowledge of the gametophyte of the Ophioglossaceæ is now pretty complete, owing to the important researches of Jeffrey (The Gametophyte of Botrychium virginianum, *Proc. Canad. Inst.* V, 1898) and Lang (On the prothalli of Ophioglossum pendulum and Helminthostachys zeylanica, *Ann. Bot.* 16, 1902). The former has described in detail the prothallium of *Botrychium virginianum*, while Lang was fortunate enough to procure fairly complete material of *Ophioglossum pendulum* and *Helminthostachys zeylanica*, so that all three genera are represented. As might be expected, there is a good deal of similarity, this being most marked between Botrychium and Helminthostachys. All agree in having a subterranean prothallium which is destitute of chlorophyll, thus resembling the prothallia of certain species of Lycopodium. It is highly improbable that this condition is a primitive one, however, and too much stress cannot be laid upon it in making a comparison with the green prothallia of the Marattiaceæ, with which otherwise there is a close agreement, especially in the case of Ophioglossum. As some species of Lycopodium have a green prothallium, and chlorophyll has been found under certain circumstances in the pro-

[1] Since this paper was written there has been published by Bower (*Ann. of Bot.* Apr. 1904) an account of a remarkable species of Ophioglossum from Sumatra, in which the leaf consists simply of a long-stalked sporangiophore with scarcely a trace of the sterile segment. This interesting plant almost realizes the hypothetical form assumed by the writer as the ancestor of the ferns.

thallium of Ophioglossum (Mettenius — *Filices Hort. Bot. Lips*, 1856), it is extremely likely that the absence of chlorophyll is a secondary condition, and that so far as the prothallium is concerned, the Marattiaceæ approach more nearly the ancestral type than do the Ophioglossaceæ.

Both Jeffrey and Lang are agreed as to the essentially fern-

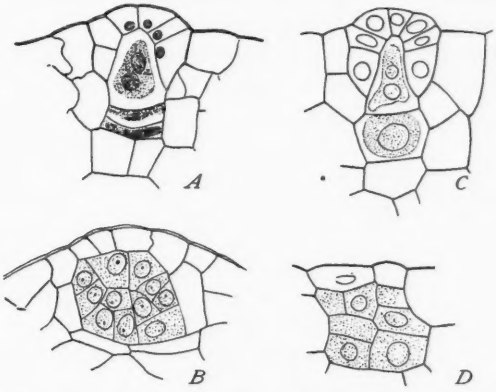

FIG. 1.—*A*, archegonium; *B*, young antheridium of *Marattia douglasii*, × 350. *C*, archegonium; *D*, young antheridium of *Ophioglossum pendulum*, × 250. *C*, *D*, after Lang.

like character of the prothallium. This is shown in its apical growth, strongly dorsiventral form, and especially in the reproductive organs, which in Ophioglossum (Fig. 1, *A*, *B*) resemble to an extraordinary degree those of Marattia. The large multiciliate spermatozoids are also entirely fern-like in form. When to the close resemblance in the sexual organs is added the marked correspondence in the development of the embryo, which is very similar to that of the Marattiaceæ and not in the least like that of Lycopodium, the case seems a very strong one.

There next remains to be considered the structure of the adult sporophyte. In most species of both Ophioglossum and Botrychium the stem is a short upright rhizome about which the leaves are spirally arranged. In *Ophioglossum pendulum*, however, and in Helminthostachys the plant is dorsiventral. Among the Marattiaceæ both types also occur. Marattia and Angiopteris are radial, Danæa is dorsiventral. Bower (*loc. cit.*,

p. 219) is inclined to consider the radial type as older than the dorsiventral, but as both types occur in both families under consideration, this has little bearing upon the question of their relationships.

In the structure of the apical meristems the Ophioglossaceæ are even more fern-like than the Marattiaceæ, as they regularly show a single tetrahedral initial in both stem and root. In this respect they resemble the leptosporangiate ferns more than they do the Marattiaceæ. In the very young sporophyte of the latter, however, the root shows a single apical cell which is replaced by a group of initials in the more massive roots of the older sporophyte.

The very complicated vascular system of the older sporophyte in the Marattiaceæ is undoubtedly associated with the massive stem. A study of the young plant shows that in the earlier stages there is a single cylindrical stele much like that which occurs in the adult rhizome of Helminthostachys and such leptosporangiate ferns as Gleichenia. This is considered by Jeffrey to be a primitive condition from which the more complicated arrangement found in the adult stem of the Marattiaceæ has been derived. The arrangement of the vascular bundles in the stem of Ophioglossum is much like that in the typical ferns, while Botrychium closely resembles Osmunda. (Jeffrey, "Structure of the Stem in the Pteridophyta and Gymnosperms," *Phil. Trans.* 195, 1902.)

The leaves of the Ophioglossaceæ, which are in some respects different from those of the typical ferns, nevertheless are much more like these than like either the lycopods or Equisetaceæ. The venation is not essentially different from that of the Marattiaceæ, and although there is never found the circinate form of the young leaf, so characteristic of the ferns, still in the larger species of Botrychium there is an approach to this which suggests that the coiling of the young leaf is connected with the very great development of the lamina of the leaf which characterize most ferns.

While the reticulate venation found in Ophioglossum is different from that in most ferns, still there are many ferns which show a very similar venation. Thus among the Marattiaceæ

there may be instanced Kaulfussia, whose venation is not very different from that of Ophioglossum, and possibly a further comparison might be made in the form of the leaf with the palmately lobed leaf of *Ophioglossum palmatum*. On the other hand, the venation of Agiopteris or Danæa is almost identical with that of Helminthostachys. (See Fig. 2.)

Farmer (Farmer & Freeman, "The Structure and Affinities of Helminthostachys," *Ann. Bot.* 1899) has referred to the stipules of the latter genus and thinks they are not directly compa-

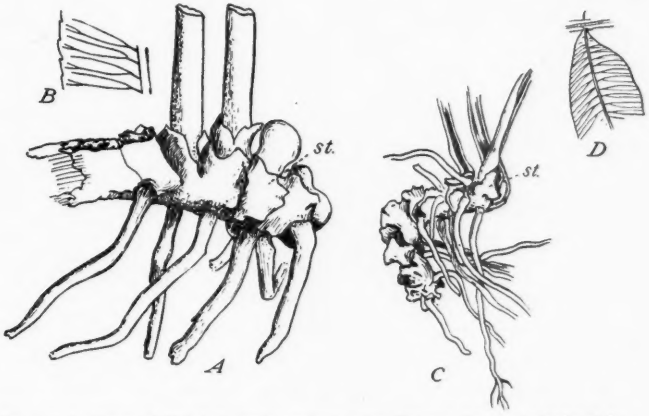

FIG. 2.—*A*, rhizome of *Helminthostachys zeylanica*, after Farmer; *B*, part of a leaflet of the same plant, showing the venation; after Hooker & Baker: *C*, Rhizome of *Danæa alata*, (reduced); *D*, base of leaflet showing venation; st., stipules.

rable to those of the Ophioglossaceæ, although it is not quite clear wherein the difference consists. There certainly seems to be no essential difference between the stipular structure at the leaf base in Botrychium (Campbell, *Mosses and Ferns*, p. 242) and those in Marattia or Danæa, although in the latter genera the stipules are more distinct. The development of stipular structures is especially marked in both Ophioglossaceæ and Marattiaceæ, while among the Leptosporangiatæ they are generally absent except in the Osmundaceæ, which are admittedly the nearest relatives among the Leptosporangiatæ to the eusporangiate ferns.

The markedly dorsiventral rhizome of Danæa is strongly sug-

gestive of that of Helminthostachys (Fig. 2, *A*, *C*), and the position of the leaves and roots is much the same. The cylindrical stelar tube with relatively small foliar lacunæ in Helminthostachys may perhaps be compared to the stele in the young rhizome of Danæa, which, according to Jeffrey, is of much the same type. (Jeffrey, *loc. cit.*, pp. 120, 121.)

The most marked histological difference between the Marattiaceæ and the Ophioglossaceæ is perhaps the occurrence of conspicuous mucilage ducts in the former. These are, however, also wanting in the other ferns. The circinate form of the young leaves is probably associated with the great development of the lamina of the leaf, but is certainly a difference of some importance.

To the labors of Bower we owe by far the most important contributions to our knowledge of the development of the sporangium that have been made for many years. These enable us to make a detailed comparison of all the developmental stages in each group, and a careful study of his descriptions and figures of the two groups in question have led me to a somewhat different result from that reached by him.

The progression from the sporangial spike of Ophioglossum to the much branched sporangiophore of Botrychium or Helminthostachys, with its numerous distinct sporangia, is comprehensible enough; but the relation of the sporangiophore of the Ophioglossaceæ to the sporangia of the other pteridophytes is not so obvious. Bower believes (*loc. cit.*, p. 250) that all pteridophytes may be reduced to the strobiloid type, this being reduced to a single sporophyll in Ophioglossum. As we have stated elsewhere, this theory seems hardly satisfactory when applied to the ferns, however probable it may appear for the other pteridophytes. The comparison of the sporangial spike of Ophioglossum to the single sporangium of Lycopodium appears rather improbable, and it seems more in accordance with the facts to consider it an entirely distinct development, derived directly from the whole upper part of the sporogonium of the ancestral form.

Bower's very complete account of the sporangia in Ophioglossum and the Marattiaceæ suggests a possible point of con-

tact between the two groups. In the very peculiar *Ophioglossum palmatum*, there may be several nearly sessile sporangiophores borne near, or actually upon, the margin of the large palmately lobed sterile segment of the leaf. Among the Marattiaceæ

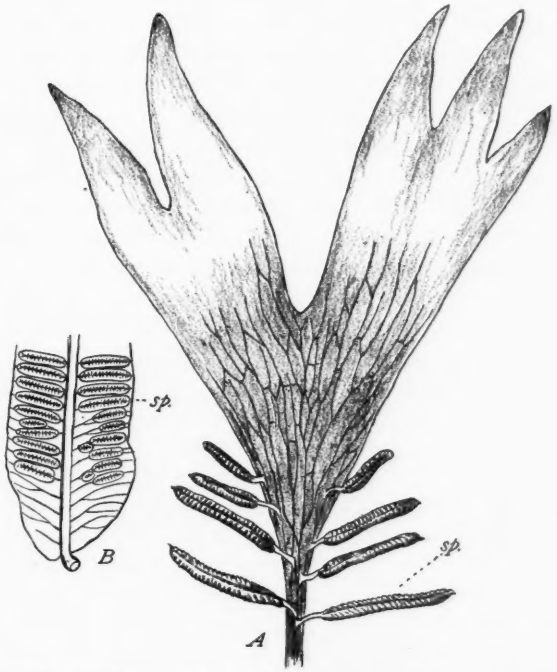

FIG. 3.— *A*, leaf of *Ophioglossum palmatum*, showing the position of the numerous sporangiophores, *sp.*, — after Bower; *B*, part of a sporophyll of *Danæa alata*, showing the elongated synangia, *sp.*; × 2.

Danæa shows a marked resemblance to Ophioglossum in the arrangement of the loculi in the greatly elongated synangia, which almost completely cover the lower surface of the contracted sporophylls. A study of the development of the sporangia in the two, to judge from Bower's account and figures, shows a close resemblance in many particulars.

Bower thinks that the elongated synangium of Danæa has been secondarily derived from a circular one, like that of Kaul-

fussia, but there is no certain evidence, either morphological or geological, that the type found in Danæa may not be the older. While a direct comparison of the sporangiophore of the existing species of Ophioglossum with the synangium of Danæa would be hardly justifiable, still it is conceivable that synangia of the type of Danæa might have originated from the complete adhesion to the surface of the sterile leaf segment of a series of small sporangiophores not so very different from those actually found in *Ophioglossum palmatum* (Fig. 3). If the primitive character of the synagium of Danæa is admitted, it is easy to trace the origin of the marattiaceous types by the expansion of the leaf lamina. Bower suggests that the primitive type of Marattiaceæ probably had an undivided leaf like that of *Danæa simplicifolia*, with scattered round sori similar to those of Kaulfussia. We agree with this except as to the character of the sori, which we believe were quite as probably like those of the actual *Danæa simplicifolia*.

In comparing the two families, Ophioglossaceæ and Marattiaceæ, it is clear that they closely resemble each other in the character of the reproductive organs and embryo, and also in the apical growth and dorsiventral form of the gametophyte. The position of the archegonia and the absence of chlorophyll are undoubtedly associated with the subterranean life of the gametophyte.

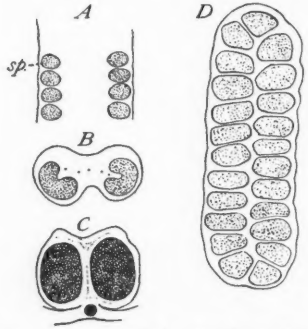

FIG. 4.—*A*, longitudinal section of part of the sporangiophore of *Ophioglossum pendulum*, × 2; *B*, cross-section of the same; *C*, cross-section of the synangium of *Danæa alata*, × 15; *D*, longitudinal section of the same.

While in the sporophyte such differences as the coiled vernation of the leaf, and presence of mucilage ducts in the Marattiaceæ must be taken into account, the two orders nevertheless agree in the general morphology of both stem and leaf, including the venation of the leaves, while in regard to the apical growth of the stem and root, the Ophioglossaceæ are more like the higher ferns than are the Marattiaceæ. Finally,

whether or not the possibility of a direct connection between the two is admitted, there is no question of the strong resemblance between the sporangia of Ophioglossum and Danæa. In view of all these facts, we can see no valid reason for removing the Ophioglossaceæ from their association with the ferns, and we believe that their association with the Marattiaceæ among the eusporangiate ferns is entirely justified.

The Marsiliaceæ.

That the Marsiliaceæ are directly allied to some group of homosporous leptosporangiate ferns is apparent; but there has been little attempt to connect them directly to any of the existing ferns. The writer (*loc. cit.*, p. 421) has suggested a comparison

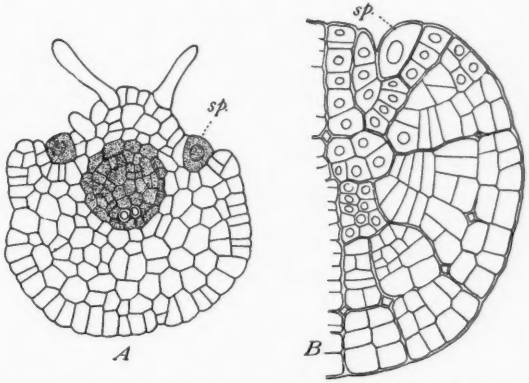

Fig. 5.—*A*, cross-section of a fertile leaf-segment of *Schizæa pennula*, highly magnified; *sp.*, sporangium mother-cell—after Prantl; *B*, cross-section of very young sporocarp of *Marsilia quadrifolia*, × 500, after Johnson. The marginal cell, *sp.*, gives rise to a row of sporangia.

with the peculiar Ceratopteris, and has also compared the antheridium with that of the Polypodiaceæ.

The more recent work of Belajeff ("Die männlichen Prothallien der Wasserfarne," *Bot. leit.*, 1898) on the antheridium, and of Johnson ("On the leaf and sporocarp of Marsilia," *Ann. Bot.* XII, 1898) ("On the leaf and sporocarp of Pilularia," *Bot. Gaz.* XXVI, 1898) and Gœbel (*Organographie der Planzen*,

Part II, 1900) upon the sporocarp, have suggested a somewhat different affinity, and it was thought worth while to look into the evidence carefully, supplementing it by a direct comparison of such material as was available.

Gœbel has called attention to the similarity between the young sporocarp of Marsilia and the fertile leaf-segment of Schizæa. Johnson's studies on the sporocarp of both Marsilia and Pilularia bear out this, and a comparison with Prantl's figures of the

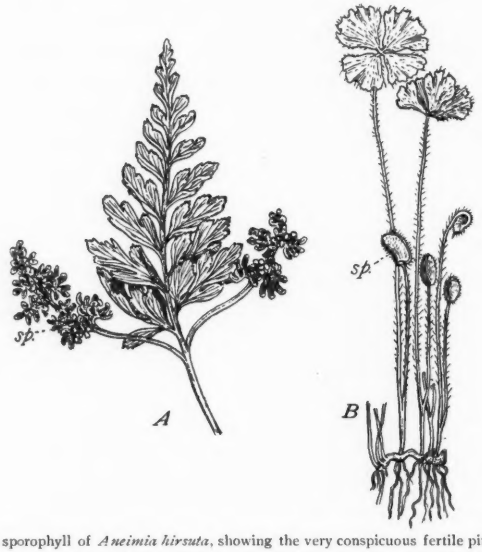

FIG. 6.—*A*, sporophyll of *Aneimia hirsuta*, showing the very conspicuous fertile pinnæ, *sp.*; *B*, Plant of *Mearsilia salvatrix*, with the long-stalked sporocarps, *sp.*, after Sachs.

young sporophytes of Schizæa emphasizes the marked resemblance between the two (Fig. 5). Johnson does not admit the foliar nature of the sporocarp; that is, he does not believe the capsule is homologous with the leaf lamina, a view which has been expressed by the writer, and which is supported by most students of the subject. A comparison of the developing fertile segment of the leaf of Schizæa, however, shows that at the time the first rudiments of the marginal sporangia appear, there is no more trace of a lamina than in a corresponding stage of the sporocarp in Marsilia. In short, the structure of the very

young sporocarp of Marsilia and the fertile leaf segment of Schizæa is remarkably similar; moreover, the origin of the sporangia from originally marginal cells is noteworthy.

The origin of the sporocarps in the Marsiliaceæ, however,

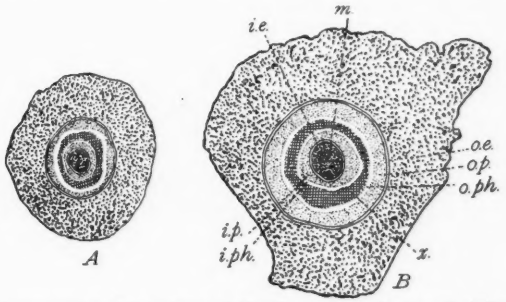

FIG. 7.—*A*, cross-section of the rhizome of *Marsilia vestita*, × about 15; *B*, similar section of the rhizome of *Aneimia hirsuta*. The outer cortical tissue is composed in both of brown sclerenchyma; the tubular stele encloses a medulla also composed of sclerenchyma; the stele has an outer (*o. e.*) and an inner (*i. e.*) endodermis, outer (*o. p.*) and inner (*i. p.*) pericycle; outer (*a. ph.*) and inner (*i. ph.*) phlœm; and a central xylem (*x*).

is different from that of the fertile leaf-segment in Schizæa, but finds a close counterpart in the allied genus Aneimia (Fig. 6) where the remarkably developed fertile pinnæ bear much the

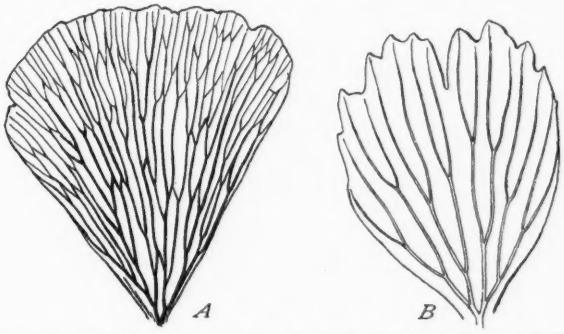

FIG. 8.—*A*, leaflet of *Nearsilia vestita*, × 10; *B*, pinnule of *Aneimia hirsuta*, × 8; both show a strictly dichotomous venation.

same relation to the rest of the leaf, that the sporocarp does in Marsilia. The pinnate form of the sporocarp in Marsilia and the dichotomous sterile segment, are comparable to what obtains

in some species of Schizæa, where the leaf is dichotomously divided, but the fertile segments are pinnate.

A comparison of the vegetative organs of the Marsiliaceæ and Schizæaceæ shows equally marked resemblances. The creeping rhizome of Marsilia and Pilularia is remarkably similar to that of Schizæa and certain species of Aneimia (Fig. 7), as may be clearly seen from the figure. The leaves also show interesting resemblances. Thus the filiform leaf of Pilularia finds its exact counterpart in the sterile leaves of *Schizæa pusilla*, while the four-lobed leaf of Marsilia is comparable to such species as *Schizæa pennula*, with dichotomously branched lamina. The venation in Schizæa and Aneimia is characteristically dichotomous, closely resembling that of Marsilia. Except in Lygodium, the pinnate venation found in the majority of the ferns does not occur among the Schizæaceæ.

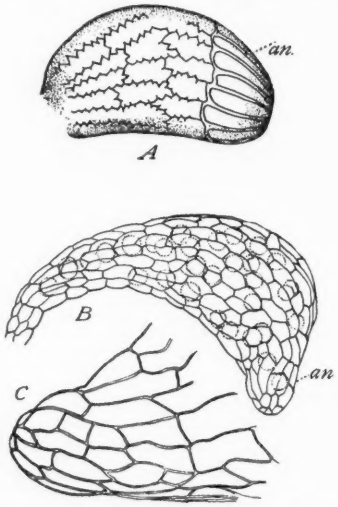

FIG. 9.—*A*, sporangium of *Schizæa pennula*, showing the apical annulus, *an.* × 45, (after Prantl), *B*, sporangium of *Pilularia Americana*; the apical region suggests the annulus of Schizæa; *C*, apical region, more enlarged.

So far as I am aware, no direct comparison of the sporangia in the two families has been made, although the early stages of the sporangium have been carefully studied. The Schizæaceæ differ from all the other ferns in the very peculiar form of the sporangium which is strongly oblique and has a terminal annulus. The sporangia of *Pilularia americana* and *Marsilia vestita* were examined, and it was found, especially in the case of the former, that the sporangia resembled strongly those of the Schizæaceæ. In Marsilia the closely packed microspore rendered it difficult to make out the form of the parietal cells, but in Pilularia the spores are widely separated and the form of the parietal cells is easily seen when the sporangia,

after placing them in water for a short time, are treated with alcohol to check the swelling of the mucilaginous cell walls which otherwise are soon completely destroyed. The oblique form of the sporangium is especially conspicuous in Pilularia (Fig. 8, *B*), and the arrangement of the cells near the apex is very suggestive of the annulus of Schizæa, although of course in these aquatic plants, no hardening of the annulus cells takes place.

This remarkable correspondence in the structure of the sporangium, taken together with the other close structural resemblances, justifies the assumption of a not very remote relationship between the Schizæaceæ and Marsiliaceæ.

It may be added that this view would tend to confirm the contention of Belajeff, that in the male gametophyte there are two antheridia, and not a single one as the present writer has held. The antheridium of the Schizæaceæ[1][2] is relatively simple in structure, and might very well be compared to each of the groups of sperm-cells in Marsilia, with its two peripheral cells.

[1] Bauke — Berträge zur keimungsgeschichte der Schizæaceæ *Prings. Jahrb.* XI, 1878.

[2] Britton, E. G. & Taylor,—A life history of Schizæa pusilla, *Bull. Torrey Bot. Club*, XXVIII, 1901.

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